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Supplement to Volume 3

PAPERS IN MARINE BIOLOGY AND OCEANOGRAPHY

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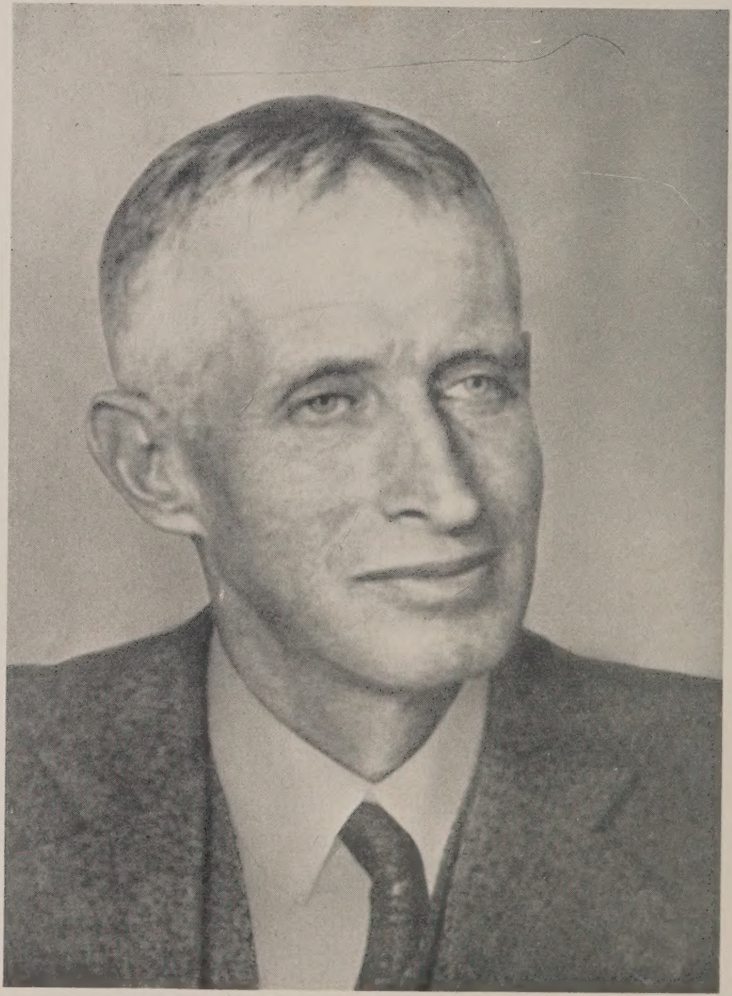

DEEP-SEA RESEARCH
Supplement to Volume 3

Papers in Marine Biology and Oceanography

Dedicated to
HENRY BRYANT BIGELOW
By His Former Students and Associates
on the occasion of
The Twenty-fifth Anniversary of the Founding
of
The Woods Hole Oceanographic Institution
1955

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FOREWORD

The papers collected in this volume have been prepared by the students, disciples and friends of Henry Bryant Bigelow, as a testimonial not only of our personal affection but to honor him for his many contributions to the advancement of oceanography.

A half century ago when Alexander Agassiz set sail for the Maldive Islands with Henry Bigelow as his assistant, oceanography in America was an interest promoted from time to time through individual initiative and, when in line with their primary duties, by appropriate governmental agencies. Today, as his latest monograph on fishes comes off the press, oceanography is a fully recognized division of science, complete with standard textbook and special journals. Its work is instrumented by half a dozen full-scale laboratories and research vessels operated by university departments or independently, and distributed equably along our coast. More important, it is a science in which a new viewpoint has developed and new vistas have opened. Of course, this has been the work of many men, but in the United States Henry Bigelow more than any other has provided the wise leadership which has insured success.

In the preface to his book, " Wind Waves at Sea, Breakers and Surf " (written with W. T. Edmondson as a contribution to the World War II effort), it is stated: " We wish it expressly understood that we have made no contributions to the theory of waves. But we would not have dared to undertake the task, if we had not observed the behavior of waves at sea, from large craft and from small, in various parts of the world, under various conditions of wind and weather; or if we had not had an opportunity to watch the development of breakers—and cope with the smaller sizes—off beaches of various shapes, off rocky coastlines, and over submerged ledges ". This insistence on personal experience as a necessary prerequisite of scientific judgment (or any other judgment for that matter) is characteristic.

By good fortune Henry Bigelow was born into a segment of New England society in which the tradition of plain living and high thinking was graced by the fruits of Yankee enterprise. Young men were expected to receive the best of education, any natural taste for outdoor life was encouraged and intellectual ambitions were not frowned upon. Summers at Cohasset, on Massachusetts Bay, gave him an instinctive knowledge of seamanship and the things of the sea. Hunting in autumn took him to all parts of the coast and the uplands as well. In winter the mountains were explored on snowshoes, and in later life on ski; the mountains are, in fact, the true love of this oceanographer. And in the spring there are trout in the New England brooks.

Thus he became the best-informed naturalist that one could hope to go afield with. His outdoor life is a routine, fixed by the seasons, and followed with the same insistence on knowing all that is to be known of the matter, which marks his more professional effort. Students of the " Physical Oceanography of the Gulf of Maine " note that the only period not covered by observations at sea coincide with the partridge season. One would no more expect him to be " at work " at that time than to find him missing on the day his course began at Harvard.

HENRY BIGELOW graduated from Harvard College, *cum laude*, in 1901. As a graduate student in zoology his doctoral dissertation, prepared under Professor E. L. MARK's guidance, was on the nuclear cycle of *Gonionemus murbachi*. Although he did not pursue cytological studies further, this was a valued experience, for from MARK he first learned the exacting requirements of scientific work. Students among us will find here the source of the discipline to which HENRY BIGELOW subjected us to our immediate chagrin but ultimate profit.

It was inevitable that HENRY BIGELOW should become a naturalist of some sort but it was not at all clear during his student days that he would become an oceanographer or even a marine biologist. His first publication was on the birds of the northeast coast of Labrador, where he had gone in company with REGINALD A. DALY and MERRITT L. FERNALD on the Brown-Harvard Expedition in the summer before his graduation. A later one was on hybrid ducks. A study of hearing in goldfish under the guidance of Professor G. H. PARKER gave him acquaintance with experimental procedures. The die was cast, however, by the opportunity to accompany ALEXANDER AGASSIZ on the voyage to the Maldive Islands, and, later on expeditions to the Eastern Tropical Pacific and to the West Indies. His duty was to care for the medusae and siphonophores collected on these voyages; and thus he gained a first-hand experience and competence in the classical disciplines of taxonomy and zoogeography which occupied the first decades of his mature career. Perhaps more important, he was introduced to the universal problems of oceanography and met first-hand the detailed tasks of scientific research at sea.

In 1912 the United States' Bureau of Fisheries and the Museum of Comparative Zoology jointly undertook a general oceanographic exploration of the Gulf of Maine which continued under HENRY BIGELOW's direction through 1924 when the field work was terminated. These explorations resulted in the publication of three superb monographs; on the fishes, the plankton, and the hydrography of the Gulf. The preparation of the first of these, on the fishes, was far advanced when interrupted by the untimely death of W. W. WELSH who had given special attention to this phase of the work, and was completed by BIGELOW at the request of the Bureau. The others are entirely his own work not only in planning and direction but in the execution at sea, in fair weather and foul, in spite of seasickness and with ships and gear far from adequate.

It is difficult to appreciate today how primitive were the resources available for this work. Thus during 1912 and 1913 reversing thermometers were accurate only to ± 0.15° C; the shortage of water bottles required repeated casts for all but the shoalest stations. Limited means were, however, more than compensated by the challenge of the unknown. He wrote:

" Few living zoologists have been as fortunate as were we on setting sail on the *Grampus* from Gloucester on our first oceanographic cruise in the Gulf of Maine on July 9, 1912, for a veritable *mare incognitum* lay before us, so far as its floating life was concerned, though the bottom fauna can be described as fairly well-known. Not but what an extensive list of pelagic crustaceans, coelenterates and other planktonic animals had been recorded thence, but everything was yet to be learned as to what groups or species would prove predominant in the pelagic fauna; their relative importance in the natural economy of the Gulf, their geographic and bathymetric variations; their seasonal successions, migrations, and annual fluctuations; their temperature affinities, whether arctic, boreal, or tropic; and whether they were oceanic or creatures of the coastal zone. We even had no idea (incredible though it may seem at this place and day) what we should probably catch when we first lowered our tow nets into deeper strata of Massachusetts Bay, for, so far as we could learn, tows had never previously been tried more than a few fathoms below its surface."

The outcome is that the Gulf of Maine is perhaps the best-known body of water of comparable size in the world; certainly the region most thoroughly explored by individual effort. Except for certain aspects which he did not examine deeply, i.e., submarine geology and sea-water chemistry, a quarter century of subsequent study added only trivial details to the picture.

During this period Henry Bigelow was the trusted advisor of the government on fisheries, a trust well earned by his first-hand knowledge of fish and fishermen, and by his incisive, direct, and ever-practical approach to human problems and his understanding of the role which science can play in their solution. A number of men later to hold important posts in the fisheries service, Herrington, Nesbit, Schroeder, Sette, and Walford, were among his students at Harvard.

In 1917–19 Henry Bigelow served as Special Expert to the U.S. Shipping Board and during 1918 the work on the Gulf of Maine was interrupted while he did his trick as navigation officer on the U.S. Army transport *Amphion*.

Of more interest in connection with scientific developments were his connections with the International Ice Patrol, established in 1913 as a result of tragic loss of life and property due to the collision of the steamship *Titanic* with an iceberg. Operation of the patrol became the duty of the U.S. Coast Guard, while the scientific studies necessary for its intelligent prosecution were directed by an interdepartmental board composed of the heads of the interested agencies. Henry Bigelow was the special consultant to the Commandant of the Coast Guard for the work of this board. During the early years of the patrol observations on plankton as well as surface temperatures and salinities, were used to trace the drift of water carrying icebergs into the shipping lanes; later the techniques of dynamic oceanography were introduced to estimate, on the spot, the velocity of the movement. As in the case of the fishery experts a succession of officers of the Coast Guard, Smith, Ricketts, Hoyle, and Graves, came to Cambridge to receive indoctrination in oceanography from Professor Bigelow. Largely as the result of his wisdom in guiding the scientific studies on which the work of the ice patrol is based, the hydrography of the northern seas is well understood and the patrol has been enabled to discharge its duties with intelligence and success.

The study of the Gulf of Maine naturally led to intimate contact with Canadians working in adjacent, and often overlapping waters. One fruit of this was a close and continuing friendship with Professor A. G. Huntsman, for many years chairman of the Biological Board of Canada; another was Bigelow's association with the North American Committee on Fishery Investigations, in which Canada, Newfoundland, France, and the United States were associated. He attended the meetings of the committee regularly between 1921 and 1933 and served as chairman at all but a few of them.

During this period Henry Bigelow formed associations with the European leaders in oceanography, marine biology, and fisheries; such men as JOHANNES SCHMIDT, JOHAN HJORT, D'ARCY THOMPSON, MARTIN KNUDSEN, HENRY MAURICE and many others still living. The esteem and affection which he won from these colleagues is nicely shown by the records of the meeting of the International Council for the Exploration of the Sea, which he attended in March 1931, as a representative of the North American Committee on Fishery Investigations and where he reported on the newly-founded Woods Hole Oceanographic Institution.

" The president . . . wished to take opportunity of his being actually present to express to him the satisfaction which his visit had caused to the Council. Dr. BIGELOW . . . had attended many council meetings and had so impressed his personality on the members and experts that the Consultative Committee had passed a recommendation . . . so important that it ought to be specially treated. In effect it contained a standing invitation to the representatives of the Woods Hole Oceanographic Institution and the North American Council on Fisheries Investigations and he might add to Dr. BIGELOW personally, whatever his future might be, to attend all meetings of the Council. The Council hoped in future to have many opportunities to consult them, to learn from them and to link up its own investigations with the work done on the western side of the Atlantic."

When in 1927 a committee of the National Academy of Sciences engaged HENRY BIGELOW as its secretary to prepare a report on the share of the United States in a world-wide program of oceanographic research, no one could have been found so well equipped by personal experience or general ability for the task. The greater part of this report, reviewing the scope, problems, and applications of oceanography, has been made public in a book entitled " Oceanography " published under his name in 1931. It is in the unpublished sections of this report, however, in which are set forth the principles that should determine the type of organization which would best remedy the then-present handicaps to the development of oceanography, that his genius for striking directly at the heart of any question and his power of exposition are superbly displayed. It is no wonder that this report was received with confidence, or that it led to the establishment of a new institution at Woods Hole and to substantial benefits to oceanography and marine biology through gifts to the Scripps Institution, the University of Washington, and the Bermuda Biological Station. And it was inevitable that the author of this report should have been asked to direct the newly-established Woods Hole Oceanographic Institution.

The principle of the ripeness of time, as applied to the appearance of prophets, is well illustrated by the history of oceanography at this period. Not only did a man emerge who had prepared himself, perhaps unwittingly, for leadership at a time when men of influence had sensed that something should be done to improve the status of marine science in America, but new ideas were in the air wafted across the ocean from a multitude of general scientific advances. HENRY BIGELOW, though trained in the classical tradition, was sensitive to these breezes, bold enough to grasp their implication, and wise enough to act on their meaning.

The following paragraphs, excerpted from a paper published in *Science* in 1930, entitled " A developing viewpoint in Oceanography ", express in BIGELOW'S own words the creed which was to guide his thinking.

" Oceanography has of late entered a new intellectual phase, to explain which a word of retrospect is necessary . . . Students of the history of science may well date the birth of modern oceanography from December 21, 1872, the day when the *Challenger* set sail from Plymouth, England, on her memorable voyage. . . . One great deep-sea expedition led to another, and more was learned about the sea during the last thirty years of the nineteenth century than had been during the preceding three thousand. But after a time, as so often happens when some scientific discipline takes a sudden spurt, this fact-finding began to lose something of its freshness.

" Students began, in short, to feel that the mere accumulation of facts from the sea, when there is an inexhaustible supply, may actually become a bit sterile, just as catching fish is to a sportsman where fish are too plentiful.——So it was natural that when persistence in the old methods no longer yielded startling discoveries, signs could be seen of the approach of a period of stagnation——. And oceanography would probably be in a moribund state in America today, just as the art of sailing a square-rigger is, but for the birth of the new idea that what is really interesting in sea science is the fitting of these facts to gether, and that enough facts had accumulated to make the time ripe for an attempt to lift the veil that had obscured (and still obscures) any real understanding of the marvelously complex and equally marvelously regulated cycle of events that take place within the sea.

" The foundation for this conscious alteration in view-point, from the descriptive to the explanatory, was a growing realization . . . that the further development of sea science the keynote must be physical, chemical and biological unity. . . .

" When one picks up a fish one may be said, allegorically, to hold one of the knots in an endless web of netting of which the countless other knots represent other facts, whether of marine chemistry, physics or geology, or other animals and plants. And just as one cannot make a fish-net until one has tied all the knots in their proper positions, so one cannot hope to comprehend this web until one can see its internodes in their true relationship. This is today the conscious aim of oceanographers."

Newcomers may feel surprise that this viewpoint had novelty, for it is still our guiding principle. But therein lies meaning.

The task of assembling a staff for the new Oceanographic Institution at Woods Hole was not an easy one for there was little raw material with which to work. There were a few young men with some experience at sea, and by combing the museums of the country doubtlessly he could have assembled a respectable group of experts on special groups of marine organisms. A primary objective, however, was to give impetus to oceanographic studies in the universities, and there was the " developing viewpoint " to be fostered. He chose the bolder course of educating a new generation drawn from the universities; physical chemists, meteorologists, physiologists, bacteriologists, whoever could be persuaded that scope for their skills could be found in studies at sea. And so the practice grew that each should make at least one short voyage at sea each season. Daily the director made his rounds, instilling little by little something of his viewpoint and wisdom on the opportunities that lay beyond the tide line. Boldness was encouraged for we were told that an oceanographer, like a turtle, made progress only by sticking his neck out.

After ten years as Director of the Woods Hole Oceanographic Institution, HENRY BIGELOW asked to be relieved. The painstaking labour of creating and guiding the development of the Institution had been a sacrifice to the general welfare, made at the expense of his own natural preference for first-hand scientific investigation. He continued to guide the Institution, at first as President of the Corporation and, now, as Chairman of the Board of Trustees, but was thereafter able to devote full time to his interests at Harvard University.

Harvard University appears to have been a bit slow in recognizing the merits of HENRY BIGELOW. Tradition has it that, during his first year of service as assistant in the invertebrate zoology laboratory, he discovered a student who had depicted a tunicate embellished with a complete set of neatly labelled mammalian viscera, based rather on " natural logic " than on direct observation. This intellectual dishonesty, or stupidity, so enraged him that the unfortunate student was told off in words so monosyllabic and unambiguous that the young assistant was never again to be permitted to have contact with the students in Harvard College. While the inference is perhaps apocryphal there is no doubt that the incident is authentic.

However this may be, so far as Harvard College was concerned HENRY BIGELOW remained relatively obscure, serving as curator and lecturer in the Museum of Comparative Zoology up to the time of the events leading to the establishment of the Oceanographic Institution. This may have resulted from the almost complete lack of intercourse between the Museum and the Department of Zoology during the period when these institutions existed under the same roof. At all events, it was a most fortunate state of affairs, for had he been burdened with the ordinary academic routine his achievements during this period would have been impossible. It is a tribute to the liberal policies of the University at that time that such great talent was enabled to fruit without distraction.

In 1931 HENRY BIGELOW became a full professor at Harvard and inaugurated a course in biological oceanography. Some years later this course passed into the hands of one of his disciples, Dr. GEORGE L. CLARKE, and BIGELOW took over instruction in invertebrate zoology. This was a task he could put his heart into for he felt that nowhere else is the wonderful diversity of form with which organisms are endowed so well displayed as among the invertebrates. His obligation as a professor to the students in Harvard College was to him most sacred. It is too bad they could not have had more of him. Those who benefitted most from his talents as a teacher (and taskmaster) were the succession of graduate students, both men and women, who had the privilege of working at his side in the Museum, and those whom he influenced by indirection at the Oceanographic Institution or wherever else he came in contact with thinking people.

As the years passed the counsel of HENRY BIGELOW, early recognized for its worth in the Museum of Comparative Zoology, became more and more influential in the Department of Biology and in Harvard University at large. On reaching the ordinary age of retirement the University asked him to continue in service, a very real honour, until the mandatory age of seventy was reached. In 1946 he was granted an honorary degree by Harvard and in the same year by the University of Oslo, similar recognition having been made by Yale University some years earlier.

Among other formal honours he is the recipient of the Johannes Schmidt Medal, the Agassiz Medal awarded by the National Academy of Sciences for contributions to Oceanography, and the Bowle Medal of the American Geophysical Union in recognition of accomplishment through cooperative effort in the advancement of the geophysical sciences. He has also been elected to membership in the National Academy, the American Academy of Arts and Sciences, and the Philosophical Society, and is affiliated with the Norske Videnskaps Academy, the Royal

Geographical Society of London, the Zoological Society of London, and the Marine Biological Society of the United Kingdom.

The crowning glory of these later years is not, however, the honours which come his way. It is the stream of publications which flowed from his pen, always in association with WILLIAM C. SCHROEDER, about fishes. This flow shows no attenuation with time; it reached, in fact, its spate after retirement from academic duty, as a glance at the appended bibliography will show. The handsome monographs on the Fishes of the North-western Atlantic show where his heart really lies, for he was free to follow its guidance once he had played his part in putting American Oceanography on its feet.

HENRY BRYANT BIGELOW, we greet you on this the twenty-fifth anniversary of the opening of the laboratory of the Woods Hole Oceanographic Institution. " We " are the authors of the papers appended hereto. If they are diverse in subject matter it is because you are catholic in the interests we share in common. If they appear disconnected it is because we have individually failed to achieve the physical, chemical, and biological unity to which you have encouraged us to aspire. " We " are also many others who have been unable to contribute a paper, for reasons which you can comprehend, but who none the less wish to join in this testimonial.

You have broadened the vision, sharpened the perception, fortified the determination, simplified the outlook, improved the standards, and corrected the folly of each of us. We continue to come to you for counsel. You have always been your own excuse for being, and to all of us it is a joy to be with you.

We hope that what is written will not offend your Yankee reticence. We know it will not inflate your pride, for that is built of something tough. You are an " individual " and we have hailed you as something of a prophet. That is a combination from which legends grow. Your legend can afford to be correct; it is not necessary to exaggerate the truth. We have followed your precepts in setting down what can be learned about you from the written word and the observed fact. In the inferences drawn and the judgments passed we hope we have not stuck the neck out too far. We will be happy if this volume pleases you.

BIBLIOGRAPHY OF HENRY BRYANT BIGELOW

(1902), Birds of the northeastern coast of Labrador. *The Auk*, **19**, 24–31.

(1904), Medusae from the Maldive Islands. *Bull. Mus. Comp. Zool., Harvard Coll.*, **39** (9), 245–269, 9 pls.

(1904), The sense of hearing in the goldfish, *Carassius auratus* L. *Amer. Natur.*, **38** (448), 275–284.

(1905), The shoal-water deposits of the Bermuda Banks. *Proc. Amer. Acad. Arts and Sci.*, **40** (15), 559–592.

(1907), On hybrids between the mallard (*Anas boschas*) and certain other ducks. *The Auk*, **24** (4), 382–388.

(1907), Studies on the nuclear cycle of *Gonionemus murbachii* A. G. Mayer. *Bull. Mus. Comp. Zool., Harvard Coll.*, **48** (4), 287–399, 8 pls.

(1909), Coelenterates from Labrador and Newfoundland, collected by Mr. Owen Bryant from July to October, 1908. *Proc. U.S. Nat. Mus.*, **37** (1706), 301–320, Pls. 30–32.

(1909), Cruise of the U.S. Fisheries Schooner *Grampus* in the Gulf Stream during July, 1908, with description of a new Medusa (Bythotiaridae). *Bull. Mus. Comp. Zool., Harvard Coll.*, **52** (12), 195–210, 1 pl.

(1909), Report on the scientific results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer *Albatross*, from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., Commanding. XVI. The Medusae. *Mem. Mus. Comp. Zool., Harvard Coll.*, **37**, 243 pp., 48 pls.

(1911), Biscayan plankton collected during a cruise of H.M.S. *Research*, 1900. XIII. The Siphonophora. *Trans. Linn. Soc., London*, (2nd ser., Zool.), **10** (10), 337–358, Pl. 28.

(1911), Report on the scientific results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer *Albatross*, from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., Commanding. XXIII. The Siphonophorae. *Mem. Mus. Comp. Zool., Harvard Coll.*, **38** (2), 173–402, 32 pls.

(1911), The work of the *Michael Sars* in the North Atlantic in 1910. (A review.) *Science*, n.s., **34**, 7–10.

(1911), Fishes and Medusae of the intermediate depths. A note on the work of the *Michael Sars*. *Nature*, **86**, 483.

(1912), Reports on the scientific results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer *Albatross*, from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, Commanding. XXVI. The Ctenophores. *Bull. Mus. Comp. Zool., Harvard Coll.*, **54** (12), 369–404, 2 pls.

(1912), Scientific results of the Philippine cruise of the Fisheries Steamer *Albatross*, 1907–1910. 22. Preliminary account of one new genus and three new species of Medusae from the Philippines. *Proc. U.S. Nat. Mus.*, **43** (1931), 253–260.

(1913), Medusae and Siphonophorae collected by the U.S. Fisheries Steamer *Albatross* in the northwestern Pacific, 1906. *Proc. U.S. Nat. Mus.*, **44** (1946), 1–119, 6 pls., 2 text figs.

(1913), Oceanographic cruises of the U.S. Fisheries Schooner *Grampus*, 1912–1913. *Science*, n.s., **38** (982), 599–601.

(1913), A new closing-net for horizontal use, with a suggested method of testing the catenary in fast towing. *Int. Rev. Ges. Hydrobiol. u. Hydrogr.*, **5**, 576–580, 8 text figs.

(1914), Explorations in the Gulf of Maine, July and August 1912, by the U.S. Fisheries Schooner *Grampus*. Oceanography and notes on the plankton. *Bull. Mus. Comp. Zool., Harvard Coll.*, **58** (2), 31–147, 9 pls.

(1914), Fauna of New England. 12. List of the Medusae Craspedotae, Siphonophorae, Scyphomedusae, Ctenophorae. *Occ. Papers, Boston Soc. Nat. Hist.*, **7**, 1–37.

(1914), Note on the medusan genus *Stomolophus* from San Diego. *Univ. Calif. Publ. Zool.*, **13** (10), 239–241.

(1914), Oceanography and plankton of Massachusetts Bay and adjacent waters, November 1912–May, 1913. *Bull. Mus. Comp. Zool., Harvard Coll.*, **58** (10), 383–420, 1 pl., 7 text figs.

(1915), *Eperetmus*, a new genus of Trachomedusae. *Proc. U.S. Nat. Mus.*, **49** (2114), 399–404, Pl. 59.

(1915), Exploration of the coast water between Nova Scotia and Chesapeake Bay, July and August, 1913, by the U.S. Fisheries Schooner *Grampus*. Oceanography and plankton. *Bull. Mus. Comp. Zool., Harvard Coll.*, **59** (4), 151–359, 2 pls., 82 text figs.

(1916), *Halimedusa*, a new genus of Anthomedusae. *Trans. R. Soc., Canada*, (3), **10** (4), 91–95, 1 pl.

(1917), Explorations of the coast water between Cape Cod and Halifax, in 1914 and 1915, by the U.S. Fisheries Schooner *Grampus*. Oceanography and plankton. *Bull. Mus. Comp. Zool., Harvard Coll.*, **61** (8), 163–357, 1 pl., 100 text figs.

(1917), Explorations of the United States Coast and Geodetic Survey Steamer *Bache* in the western Atlantic, January–March 1914 under the direction of the United States Bureau of Fisheries. Oceanography. *U.S. Bur. Fish. Doc.* 833 (App. 5 to Rept. U.S. Comm. Fish. for 1915), 1–62, 53 text figs., 1 fold-in.

(1918), Some Medusae and Siphonophorae from the western Atlantic. *Bull. Mus. Comp. Zool. Harvard Coll.*, **62** (8), 365–442.

(1919), Hydromedusae, siphonophores and ctenophores of the *Albatross* Philippine Expedition. Contributions to the biology of the Philippine Archipelago and adjacent regions. *Bull. U.S. Nat. Mus.*, 100, **1** (5), 279–362, Pls. 39–43.

(1920), Medusae and ctenophores from the Canadian Arctic Expedition, 1913–1918. *Rept. Canadian Arctic Exped.*, 1913–1918, **8** (H), 22 pp., 2 pls.

(1922), Exploration of the coastal water off the northeastern United States in 1916 by the U.S. Fisheries Schooner *Grampus*. *Bull. Mus. Comp. Zool., Harvard Coll.*, **65** (5), 85–188, 53 text figs.

(1925), Oceanic circulation. *Science*, 62, 317–319.

(1925), Recent oceanographic work carried on jointly by the Museum of Comparative Zoology and by the U.S. Bureau of Fisheries. *Bull. Nat. Res. Council*, No. 53, 69–70.

(1926), Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 1–509, 134 text figs.

(1927), Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 511–1027, 207 text figs.

(1927), Dynamic oceanography of the Gulf of Maine. *Bull. Nat. Res. Council*, No. 61, 206–211.

(1928), Exploration of the waters of the Gulf of Maine. *Geogr. Rev.*, **18**, 232–260.

(1928), Scyphomedusae from the Arcturus Oceanographic Expedition. *Zoologica, N.Y. Zool. Soc.*, **8** (10), 495–524, Figs. 180–184.

(1929), Museum of Comparative Zoology. Its cooperation with the International Ice Patrol and the U.S. Bureau of Fisheries. *Harvard Alumni Bull.*, **31**, 433–434.

(1930), A developing view-point in oceanography. *Science*, 71 (1830), 84–89.

(1930), The Woods Hole Oceanographic Institution. *Harvard Alumni Bull.*, **32**, 749–750.

(1930), The Woods Hole Oceanographic Institution. *Science*, **71**, 277–278.

(1930), The Woods Hole Oceanographic Institution. *J. du Cons.*, **5** (2), 226–228.

(1931), Siphonophorae from the Arcturus Oceanographic Expedition. *Zoologica, N.Y. Zool. Soc.*, **8** (11), 525–592, text figs. 185–220.

(1931), Oceanography; its scope, problems and economic importance. Houghton Mifflin Co., N.Y., and Boston, 263 pp.

(1933), Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. 1. The cycle of temperature. *Pap. Phys. Oceanogr. Meteorol.*, **2** (4), 1–135, 66 text figs.

(1938), Plankton of the Bermuda Oceanographic Expeditions. VIII. Medusae taken during the years 1929 and 1930. *Zoologica, N.Y. Zool. Soc.*, **23** (2), 99–189, 23 text figs.

(1940), Eastern Pacific Expeditions of the New York Zoological Society. XX. Medusae of the Templeton Crocker and Eastern Pacific " Zaca " Expeditions, 1936–1938. *Zoologica, N.Y. Zool. Soc.*, **25** (3), 281–321, text figs 1–20.

(1952), Thomas Barbour. *Biogr. Mem., Nat. Acad. Sci.*, **27**, 13–45.

Bigelow, H. B. and Edmondson, W. T. (1947), Wind waves at sea, breakers and surf. *U.S. Navy Hydrogr. Office Pub.* 602, xii plus 177 pp., 57 text figs., 24 pls. (Also translated into Russian in 1951 by B. B. Shtokgana.)

Bigelow, H. B. and Farfante, I. P. (1948), Fishes of the Western North Atlantic. Chap. 1. Lancelets. *Mem., Sears Found. Mar. Res.*, **1**, 1–28, 3 text figs.

Bigelow, H. B. and Iselin, C. (1927), Oceanographic reconnaissance of the northern sector of the Labrador current. *Science*, **65** (1691), 551–552.

Bigelow, H. B. and Leslie, Maurine (1930), Reconnaissance of the waters and plankton of Monterey Bay, July 1928. *Bull. Mus. Comp. Zool., Harvard Coll.*, **70** (5), 429–481, 43 text figs.

Bigelow, H. B., Lillick, Lois C. and Sears, Mary (1940), Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. 1. Numerical distribution. *Trans. Amer. Phil. Soc.*, n.s., **31** (3), 149–191, 10 text figs.

Bigelow, H. B. and Schroeder, W. C. (1927), Notes on northwest Atlantic sharks and skates. *Bull. Mus. Comp. Zool., Harvard Coll.*, 68 (5), 239–251.

Bigelow, H. B. and Schroeder, W. C. (1929), A rare Bramid fish (*Taractes princeps* Johnson) in the northwestern Atlantic. *Bull. Mus. Comp. Zool., Harvard Coll.*, **69** (2), 41–50, 1 pl.

Bigelow, H. B. and Schroeder, W. C. (1934), Canadian Atlantic Fauna. 12. Chordata. 12d Marsipobranchii (Lampreys). 12e Elasmobranchii (Sharks and rays). 12f. Holocephali (Chimaeroids). Univ. Toronto Press for Biol. Bd., Canada, 38 pp., 35 text figs.

Bigelow, H. B. and Schroeder, W. C. (1935), Two rare fishes, *Notacanthus phasganorus* Goode and *Lycichthys latifrons* (Steenstrup and Hallgrimsson), from the Nova Scotian banks. *Proc. Boston Soc. Nat. Hist.*, **41** (2), 13–18, Pl. 3.

Bigelow, H. B. and Schroeder, W. C. (1936), Supplemental notes on fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **48** (*Bull No.* 20), 319–343.

Bigelow, H. B. and Schroeder, W. C. (1937), A record of *Centrolophus niger* (Gmelin) from the western Atlantic. *Copeia*, **1937** (1), 61.

Bigelow, H. B. and Schroeder, W. C. (1939), Notes on the fauna above mud bottoms in deep water in the Gulf of Maine. *Biol. Bull.*, **46** (3), 305–324, 8 text figs.

Bigelow, H. B. and Schroeder, W. C. (1940), Notes on New England fishes *Carcharodon carcharias* (Linnaeus). *Copeia*, **1940** (2), 139.

Bigelow, H. B. and Schroeder, W. C. (1940), Some deep sea fishes from the North Atlantic. *Copeia*, **1940** (4), 231–238.

Bigelow, H. B. and Schroeder, W. C. (1940), Sharks of the genus *Mustelus* in the western Atlantic. *Proc. Boston Soc. Nat. Hist.*, **41** (8), 417–438, Pls. 14–19.

Bigelow, H. B. and Schroeder, W. C. (1941), *Cephalurus*, a new genus of Scyliorhinid shark with redescription of the genotype *Catulus cephalus* Gilbert. *Copeia, 1941* (2), 73–76, 4 figs.

Bigelow, H. B. and Schroeder, W. C. (1944), New sharks from the western North Atlantic. *Proc. New England Zool. Club*, **23,** 21–36, Pls. 7–10.

Bigelow, H. B. and Schroeder, W. C. (1945), Guide to commercial shark fishing in the Caribbean area. Anglo-American Caribbean Commission, Washington, D.C., 149 pp., 56 figs. (Also, *Fishery Leaflet, U.S. Fish and Wildlife Service No.* 135.)

Bigelow, H. B. and Schroeder, W. C. (1948), New genera and species of Batoid fishes. *J. Mar. Res.*, **7** (3), 543–566, Figs. 1–9.

Bigelow, H. B. and Schroeder, W. C. (1948), Fishes of the Western North Atlantic. Ch. 2. Cyclostomes. Ch. 3. Sharks. *Mem., Sears Found. Mar. Res.*, **1** (1), 29–546. 103 text figs.

Bigelow, H. B. and Schroeder, W. C. (1950), New and little known cartilaginous fishes from the Atlantic. *Bull. Mus. Comp. Zool., Harvard Coll.*, **103** (7), 385–408, 7 pls.

Bigelow, H. B. and Schroeder, W. C. (1951), A new genus and species of Acanthobatid skate from the Gulf of Mexico. *J. Washington Acad. Sci.*, **41** (3), 110–113, 1 text fig.

Bigelow, H. B. and Schroeder, W. C. (1951), Three new skates and a new chimaerid fish from the Gulf of Mexico. *J. Washington Acad. Sci.*, **41** (12), 383–392, 4 text figs.

Bigelow, H. B. and Schroeder, W. C. (1952), A new species of the cyclostome genus *Paramyxine* from the Gulf of Mexico. *Breviora*, No. 8, 10 pp., 6 text figs.

Bigelow, H. B. and Schroeder, W. C. (1953), Fishes of the Gulf of Maine. First Revision. *Fish and Wildlife Service, Fish. Bull.*, **53** (*Fish. Bull.* 74), 1–577, 288 text figs.

Bigelow, H. B. and Schroeder, W. C. (1953), Fishes of the Western North Atlantic. Ch. 1. Sawfishes, Guitarfishes, Skates and Rays. Ch. 2. Chimaeroids. *Mem., Sears Found. Mar. Res.*, **1** (2), 588 pp., 127 text figs.

Bigelow, H. B. and Schroeder, W. C. (1954), Deep water elasmobranchs and chimaeroids from the northwestern Atlantic slope. *Bull. Mus. Comp. Zool., Harvard Coll.*, **112** (2), 37–87, 7 text figs.

Bigelow, H. B. and Schroeder, W. C. (1954), A new family, a new genus and two new species of Batoid fishes from the Gulf of Mexico. *Breviora*, No. 24, 16 pp., 4 text figs.

Bigelow, H. B. and Schroeder, W. C. (1955), Occurrence off the Middle and North Atlantic United States of the offshore hake *Merluccius albidus* (Mitchill) 1818, and of the blue whiting *Gadus (Micromesistius) Poutassou* (Risso) 1826. *Bull. Mus. Comp. Zool., Harvard Coll.*, **113** (2), 205–226, 3 text figs.

Bigelow, H. B., Schroeder, W. C. and Springer, Stewart (1943), A new species of *Carcharinus* from the western Atlantic. *Proc. New England Zool. Club*, **22,** 69–74.

Bigelow, H. B., Schroeder, W. C. and Springer, Stewart (1953), New and little known sharks from the Atlantic and from the Gulf of Mexico. *Bull. Mus. Comp. Zool., Harvard Coll.*, **109** (3), 213–276, 10 text figs.

Bigelow, H. B. and Sears, Mary (1935), Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. II. Salinity. *Pap. Phys. Oceanogr. Meteorol.*, **4** (1), 1–94, 55 text figs.

Bigelow, H. B. and Sears, Mary (1937), H 2. Siphonophorae. *Rept. Danish Oceanogr. Exped.*, 1908–10, *to the Mediterranean and Adjacent Seas*, **2** (Biol.), 144 pp., 83 text figs.

Bigelow, H. B. and Sears, Mary (1939), Studies of the waters of the continental shelf. Cape Cod to Cape Hatteras. III. A volumetric study of the zooplankton. *Mem. Mus. Comp. Zool., Harvard Coll.*, **54** (4), 183–378, 42 text figs.

Bigelow, H. B. and Welsh, W. W. (1925), Fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (1), 1–567, 278 text figs.

Barbour, Thomas and Bigelow, H. B. (1944), A new giant Ceriatid fish. *Proc. New England Zool. Club*, **23,** 9–15, Pls. 4–6.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 1-6.

Effect of trawling on animals of the sea bed

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Summary—Damage to fish food species trawled over in the main area of the North Sea plaice, cannot be serious; otherwise there would be a noticeable difference where trawling is impossible, as close to light vessels or among the under-water sand dunes.

Direct attack, covering the ground some five or six times over on the average, did break full-grown Heart Urchins, *Echinocardium cordatum*, and possibly swimming or paddler crabs (*Portunus depurator*), but appeared not to damage *Ophiura albida*, nor any of the fragile-shelled plaice food animals: razor shells, *Mactra* or *Tellina*. Those forms were not very abundant, but all the 15 specimens taken of fragile animals (other than urchins and paddlers) were undamaged. Such large urchins as were damaged were not plaice food.

Doubtless *Sabellaria* habitations (ross) would be broken and laid low, but they would probably soon be reconstructed.

Trawling, even with a tickler chain, seems again to escape the so viable indictment.

INTRODUCTION

Many trawlermen are sure that their work alters the bed of the sea. Some say that it improves it, increasing the growth of animal forms growing up from the sea bed by clearing out old structures. Others say that trawling, especially with tickler chains, harms the food of fishes by breaking protective shells and structures.

The complaint of damage is an old one. In 1376 the Commons petitioned the King of England " that the great and long iron of the wondyrchoun runs so heavily and hardly over the ground when fishing that it destroys the flowers of the land below water there ". In the 19th century the beam trawl came in for similar criticism, which Dr. W. C. MacIntosh, acting for the Royal Commission of 1863, disposed of. However, trawls have become heavier and tickler chains more common, in certain fisheries almost universal. One such fishery is the English one for plaice in the southern North Sea; and in 1938 it seemed worth while to devote a little research-vessel time to finding out whether tickler chains had any marked effect.

Doubtless trawling with heavy tickler chains breaks up and flattens structures made of sand-tubes by *Sabellaria*, and similar comparatively fragile highly projecting structures, when these are not so strong as to prevent trawling because of the frequency of tearing. But *Sabellaria* tenements seem to be annual growths, run up fairly quickly, so that it may not be assumed that much permanent damage is done.

The fishing skipper of the *George Bligh* advised that it would be foolish and not really relevant to experiment on Sabellaria grounds, which he thought to be limited compared with the whole plaice area; so the decision was made to confine the enquiry to the usual clean, sandy ground frequented by plaice.

METHODS

The first line of approach was to assume that there exists a small sanctuary about three-quarters of a mile in radius centred on each light vessel, within which trawling would be very rare, for fear of fouling the lightship's moorings. If trawling had made an appreciable effect on the benthos of the plaice area, the community within that sanctuary should be appreciably different from the community outside. The sanctuaries of two light vessels, the *Haaks* and the *Terschelling*, were examined with the following gear: Petersen's grab; Naturalist's dredge; Agassiz trawl; otter trawl with shrimp-net cover on the codend. Control hauls were made 5 miles away from the *Haaks* only. That work was done on the 6th, 7th, 8th and 9th of July, 1938. (*George Bligh* K 1938, Stas. 2–10, 11–12, 13–14).

Table I.—Dredging before and after trawling

BEFORE

George Bligh, Cruise K (1938), Sta. 16, 10th July, 1938, Naturalist's dredge (6 foot) lined shrimp-netting, Egmont SE'ly 15 miles, Dhan on 90 fms. wire in Lat. 52° 44½′ N. Long. 4° 16′ E., 13 fathoms, sand, 1015 to 2010 hours, tides various, sea 4, wind SW'ly 4, sky cloudy, 14 hauls driving with wind and tide except where otherwise noted.

Haul	*Time* (assumed 10 mins. duration)	*Dhan bearing and distance*
1	1038–1048	N to NxW ¼ mile (magnetic variation 9° W)
2	1110–1120	S to S¼E ¼ mile
3	1145–1155	S 1¼ miles
4	1235–1245	E to SE½E ½ mile
5	1314–1324	W to SWxW ½ mile
6	1356–1406	NE 200 yds. to ½ mile (? direction reversed)
7	1440–1450	NE x E to SxW½W ¼ mile
8	1519–1529	NExE ½ mile to ESE ⅛ mile
9	1551–1601	NExE ¼ mile to 200 yards
10	1623–1633	NExE ¼ mile " tide getting less "
11	1654–1704	NExE ¼ mile to ENE ⅛ mile
12	1725–1755	NExE to SW ¼ mile
13	10 minutes	NExE to SW ¼ mile " with help of engines "
14	10 minutes	buoy to NE'ward no distance

AFTER

42 traverses with the trawl as nearly as possible to the tracks of Sta. 16, Hauls 7–13; Cruise K 1938, Sta. 20, 13th July, 1938, otherwise as for Sta. 16 but time 1415 to 1920 hours, tide " 1400, Buffs and Dhan NNW, so proceeded to buoy ", sea 2, wind variable 2, sky cloudy, 7 hauls driving with wind and tide.

Haul	*Time* (assumed 10 mins. duration)	*Dhan bearing and distance*
1	1418–1428	NExN to ESE ¼ mile
2	1447–1505	NNE to S ¼ mile
3	1524–1538	NExE to S ¼ mile
4	1599–1612	NExE to S½E ¼ mile
6	no record—" foul haul "	
6	1704–1712	ENE 300 yards to SSW 200 yards
7	1730–1745	NExE to SxE ¼ mile
8	1810–1826	ENE ¼ mile to SSE 200 yards
9	1842–1900	" ? washed it all out "

Another sanctuary is provided by the under-water sand dunes of the extreme south-eastern North Sea. These are dangerous to otter trawls, because of the trawl doors getting down into the small valleys between the ridges and the net then fouling the intervening crest. The beam trawls formerly used could generally get along safely, presumably because the beam took the blow of the sand-crest. By 1939, beam trawls were almost extinct, so the " bank " area provided another sanctuary. Had trawling had an appreciable effect, the benthos should be different as one left the bank area. On July 23rd and 24th, 1939, this was investigated near the northern boundary, as located by echo-sounding, using Petersen's grab and the Naturalists' dredge. Two lines of stations were completed (*George Bligh* L 1939, Sta. 14, Hauls 0–9, Sta. 15, Hauls 0–6).

Another line of approach was to try to damage animals of the sea-bed with a trawl armed with a heavy tickler-chain. The idea was to choose a bed of some animal with a fragile shell, as fragile as possible, and then tow over it as precisely as possible.

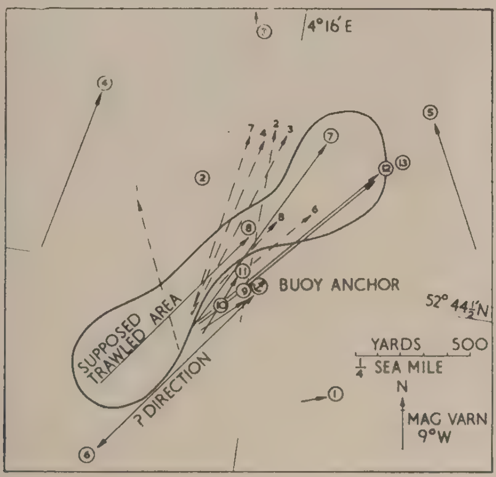

Fig. 1. Dredge hauls before and after trawling

Tracks of hauls before using trawl and tickler chain are shown as whole arrows with the serial number in a circle; hauls after, as broken arrows with unringed serial numbers, related to the position of a buoy's anchor. " Before " hauls 7 to 10 showed a bed of Heart Urchins, which was also sampled by " after " hauls 2 to 8 with moderate success, the wind having changed. The swinging positions of the buoy have been taken into account. Its area of 180 yards radius limited trawling, probably to something like the shaped area indicated. In the waist, the area would be trawled over on, the average, about 5 times. Heart Urchins were broken, but not Mactra.

Range judged visually was perhaps accurate to within 20 per cent; but the buoy's position (on 90 fms. wire in 13 fms.) would alter with the tide. A trawl, which probably fished at something over 20 yards width, was furnished with half-inch chain extending for 100 feet between the otter-boards, shorter and therefore mostly ahead of the 120 foot ground-rope. This was towed up and down on the 11th, 12th, and 13th July, 1938, crossing the ground 42 times; but owing to the error in the buoy's position due to tide and the imprecision of trawling, these cannot be thought of as 42 exactly superimposed hauls 20 yards wide. Instead we must think of an area like that shown in Fig. 1, representing fishing as close to the buoy's moorings as the ship dare go. The waist of the constricted area is 150 yards wide, which allows for 7 to 8 strips side by side; so, on the average, the ground would be swept about 5–6 times. It was possible to be more precise about the examination of the benthos bed before and after the trawling, by choosing the same phase of the tide. The animal tested was *Echinocardium cordatum*, the Heart Urchin, which was the most vulnerable animal we encountered—certainly not a plaice food at the size (from memory, about an inch and one-half in diameter), but no better animal was found. It had the further disadvantage that dredge catches would fall from 39 in a 10 minute haul to 3 when the tide slackened. This leads to an investigation of where exactly the dredge hauls lay (Table I).

The dredging ground (52° 44½′ N., 4° 16′ E.) was some 13 miles southerly of the *Haaks* Light Vessel, and because many of the hauls were made while the *George Bligh* was driving with wind and tide it is possible to plot the approximate tidal pattern (Sta. 16, Hauls 1–13, but discarding No. 6, for which the record is suspect). Assuming as a first approximation that the Dhan buoy did not swing during a 10 minute dredge haul, the course of the haul can be plotted out from the bearing and distance at the beginning and end of the haul, taking an arbitrary position for the buoy. Then, as a second approximation, the buoy is assumed to be on that bearing and at a distance of 180 yards (90 fms of wire in 13 fms of depth) from its anchor. The position of dredge haul is then replotted from the assumed true position of the buoy. Most positions of the buoy were found to lie near a N.E. and S.W. zone (magnetic), not very different from that derived from tidal information on admiralty chart 2182A for a position 52° 36′ N., 4° 10′ E.

The information given in Table I has been plotted on Fig. 1, from which it is seen that there is reasonable overlap of Sta. 16, Hauls 7–13 with Sta. 20, Hauls 2–8. Neither set lay perfectly in the trawlable area; but both lay partly within it. Sta. 16, Hauls 7–13, and Sta. 20, Hauls 1–8, may be said to do so.

Some benthos material was preserved from these investigations; but none is to be found 17 years later. It is thought that the jars were buried for safety of staff in 1940, and discarded as not in good order in 1945. Data are therefore in the form of incomplete identifications written in the log-books at the time. They are so given here.

During the attempt to break *Echinocardium* it was found possible to distinguish whole, broken or even fragmentary specimens, as " dead ", meaning " long dead " (having no spines), " recently dead " (having lost some spines), and " broken " (having all the proper spines). By counting fragments containing apical pores, it was possible to estimate the number of whole urchins.

RESULTS

The sanctuaries from trawling showed no marked difference in benthos from outside, so there seems no reason to burden this paper with details of the results. The only point of interest was a bed of *Echinocardium* within three-quarters of a mile of the *Haaks* Light Vessel, but because this did not extend around the Light Vessel, we can hardly attribute significance to it, especially because later on we found a localized bed 13 miles away in the fishing area. The fauna also included " flat stars " (*Astropecten*), *Asterias rubens*, *Portunus depurator*, *Eupagurus*, and a few *Mactra*, *Venus*, and razor-shells. These showed no marked differences three-quarters of a mile and 5 miles from the *Haaks* Light Vessel, and the species and quantities three-quarters of a mile from the *Terschelling* Light Vessel seemed similar to those close to the *Haaks*.

Similarly, there was no appreciable change in fauna taken in grab and dredge on stations 3 miles apart running out of the protected " banks " area and in to it again. The fauna was similar to that noted above.

On the other approach—the direct attack with the tickler chain and trawl—the results are shown in Table II. It will be remembered that Hauls 7–13 of the first station and Hauls 1–8 of the second, were more or less in the trawled area. It is clear that after trawling there was a new phenomenon in the catches, namely Heart Urchins recently dead and broken. Possibly there is a similar phenomenon in Paddlers (*Portunus depurator*); but in no other form is there any sign of damage.

Table II.—Dredge catches before and after trawling

	*Heart Urchins**						*Paddlers†*						*Other fragile forms*
	Live		*Recently Dead*		*Dead*		*Live*		*Recently Dead*		*Dead*		*Mactra*, Razor-shells, *Tellina*, or *Ophiura albida*, unbroken except where noted. Other forms undamaged included *Asterias rubens*, *Astropecten*, Venus and Hermit Crabs
	whole	‡broken	whole	‡broken	whole	‡broken	whole	broken	whole	broken	whole	broken	
Sta. 16 Haul					*Preliminary hauls*								
1		1											1 Ophiura
2	1												
3	2												
4	6°						3						4 Ophiura, 2 Tellina
5	3						3						1 Tellina
6	4						3						3 Ophiura
					Before trawling								
7	17	24					3						3 Ophiura, 2 Mactra
8	10	27					4						2 Ophiura, 1 Razor, 2 Mactra (1 broken)
9	17°	21					4						2 Ophiura, ** 2 Mactra, 2 Tellina
10	12	27					2						1 Mactra, 2 Tellina
11		1					1						1 Razor
12	3		9				2						4 Ophiura, 1 Mactra
13			1				3						2 Ophiura
14	1												
Sta. 20 Haul					*After trawling*								
1	4	5	1				3						2 Ophiura, 1 Mactra, 1 Razor, 1 Tellina
2	1	1	1	7			5						1 Ophiura, 1 Razor
3		Foul haul											
4				2						3			4 Ophiura
5		Foul haul											
6		1	1	3			4				1		1 Ophiura
7		1		1		1	3				1		
8	4	3		2			2						2 Ophiura, 1 Mactra
9					nil, possibly washed out								

* *Echinocardium cordatum*
‡ including fragments equivalent to one, by apical pores
° and 1 very small
† *Portunus depurator*
** 5 cms.

It may be noted that the 9 dead whole urchins taken in Haul 12 of Station 16 constitute one of those observations that one so frequently wishes one had not made.

They do not upset the remainder of the results (not being broken), but they are intrinsically difficult to account for. In the cruise report I noted them as " presumably thrown overboard after previous hauls ". I can do no better now; but only regret the long chance that delivered them on board again, if indeed that is the explanation.

REFERENCES

Dalhousie Commission (1885), *Report of the Dalhousie Commission: Trawl Net and Beam Trawl Fishing*, XXXV.
MOORE, S. A. and MOORE, H. S. (1903), *The History and Law of Fisheries*, 175.
VAN VEEN, JOH. (1935), Sand waves in the North Sea. *Hydrogr. Rev.*, 12 (1), 21.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 7-11.

A further example of the patchiness of plankton distribution

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Summary.—32 consecutive plankton samples were taken by identical tow-nets in a straight line covering a total distance of nearly 11 miles. A marked patchiness was demonstrated for all animals occurring in sufficient numbers. The results are considered in relation to those of some other such samplings already published.

IN JANUARY 1927, when the Royal Research Ships *Discovery* and *William Scoresby* were making a survey of the plankton of the sub-antarctic whaling grounds round the island of South Georgia, two series of consecutive net hauls were taken to find out how patchy in distribution were the main elements in the macroplankton. One series consisted of 23 samples and the other of 48. The results, showing a marked patchiness, particularly in the distribution of *Euphausia superba* and the amphipod *Parathemisto gaudichaudi*, were published by HARDY and GUNTHER (1935, pp. 255–263). A similar series of 32 consecutive samples were taken further to the south in the Bransfield Strait off Graham Land by the *Discovery* in April of the same year. As this series lay far outside the region of the South Georgia survey the results were not included in the former report and have not hitherto been published. Knowing that Professor BIGELOW was much interested in the matter of uneven plankton distribution I have thought that, small as it is, this additional evidence of patchiness might not be an inappropriate contribution to this volume in his honour; I wish it could have been a larger study, but it is the only piece of marine work that I have at the moment ready for immediate publication.

The series of samples now to be described was taken by the *Discovery* on April 7th, 1927, at Station 207 which lay some fifteen miles south of Livingstone Island; the exact positions at the beginning and end of the observations were respectively 62° 54′ 00″ S., 59° 50′ 30″ W. and 62° 49′ 30″ S., 60° 10′ 30″ W. The procedure adopted was the same as that on the two earlier occasions except that the nets used were of 70 cm diameter instead of the larger 100 cm diameter nets used formerly; a detailed description of these nets (N70H and N100H) will be found in KEMP and HARDY (1929, pp. 183–185). Two nets, exactly similar to each other in every particular, were used. The first net was lowered away from the starboard quarter and towed just below the surface for exactly 10 minutes at a speed of 2 knots and then hauled in; as this net was coming in, the second net was lowered away from the port quarter and towed for a similar period. Whilst this net was being towed the first net was washed down, the bucket emptied and replaced and the net got ready for reshooting; then as the second net came in at the end of its ten minutes the first net went out again. In this manner the sampling was continued to give a series of 32 consecutive hauls each beginning just as the one before it ended so that a continuous line of observation (except for one four-minute gap) was made over a distance of nearly 11 miles. The sampling began at 0300 hrs and ended at 0824 hrs; there was a loss of 4 minutes between sample 30 and 31 due to one of the nets being torn and having to be replaced by a new one. At the speed of 2 knots each sample represented a haul covering a distance of one-third of a mile.

It might perhaps be thought that there was little need for further studies of patchiness of the kind here described since the automatic plankton recorder is always taking

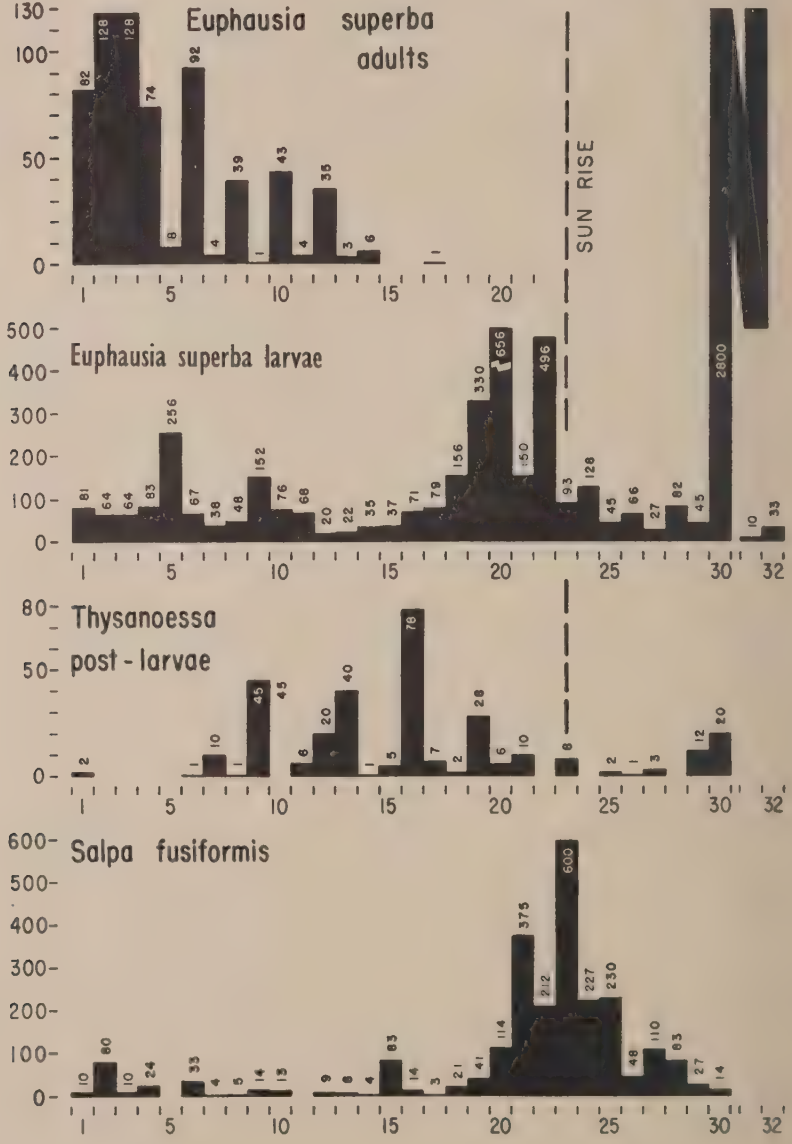

Fig. 1. Histograms showing the varying numbers of some plankton animals in thirty-two consecutive net hauls taken just below the surface at the *Discovery* station 207; each haul was of 10 minutes duration and covered a distance of one-third of a mile. For further details see text.

series of continuous samples and often revealing marked unevenness in distribution. The plankton recorder, however, because it samples continuously on an ever-moving banding, cannot show the real degree of patchiness; each section of the banding

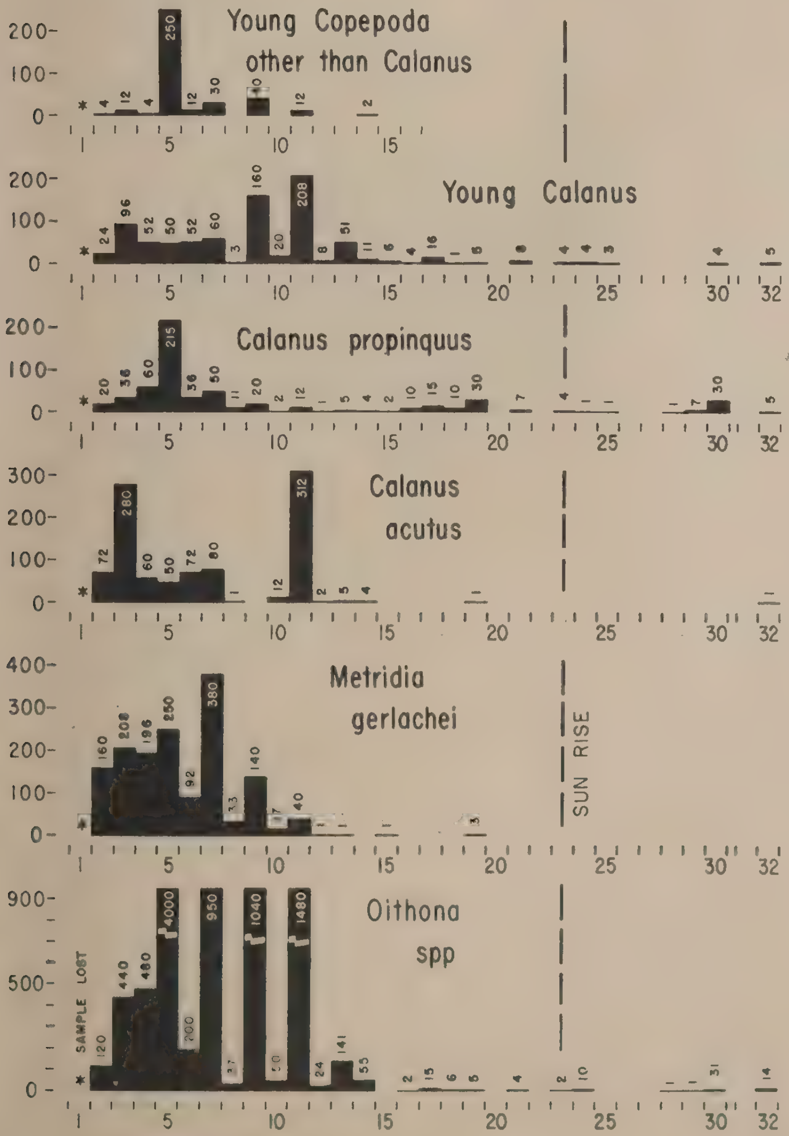

Fig. 2. Histograms showing the varying numbers of the more important copepods in the same series of consecutive net hauls in Fig. 1. The first sample was unfortunately lost by a tube breakage before the analysis had been made.

represents the passage of several miles of sea, so that any marked variation in numbers appearing from the analysis of the records is really showing itself through a considerable " smoothing of results " effected by the very nature of the sampling (Hardy, 1936 a, p. 495). The recorder was, of course, in part designed to overcome the errors due to patchiness which may falsify the results of an ordinary net survey. As far as I am aware no other experiments of the kind here described have been made except those in the South Georgia survey already referred to, and two series taken to test the validity of the plankton recorder method: one in the open South Atlantic midway between Gough Island and Cape Town (Hardy, 1936 b, p. 535) and the other in the North Sea (Hardy and Ennis, in an appendix to Hardy, 1936 a). I believe more such experiments might be valuable in the understanding of planktonic ecology.

The results of the series here published may be shown most easily in graphical form by the use of histograms and so save much description in the text. They are shown in Figs. 1 and 2, and include only those animals of which over 50 have occurred in a single sample; the remainder, including ctenophores, several kinds of amphipod, other species of copepods, and *Euphausia frigida* were present in only insignificant numbers. Instead of giving the data in tabular form as well as graphically, the actual numbers are inserted against the appropriate histograms. Apart from the marked unevenness of distribution, the effect of vertical migration is clearly seen in the case of the *Euphausia superba* adults and the copepods. The series began in darkness and ended in daylight, sunrise being at 0645, i.e. in the middle of sample 23; we see the animals just mentioned gradually withdrawing from the surface as dawn approaches. It would be valuable, but difficult, to operate such a series of consecutive nets at lower levels, for they would have to be opened and closed at the end of each haul. Regarding the many possible causes of patchiness I still believe that some of the factors suggested in the section on the dynamics of distribution in Hardy and Gunther (*loc. cit.*, pp. 343–356) are likely to be important. More observations in the field are required and particularly more experiments specially designed to test the different hypotheses; further discussion must await the results of such work.

Apart from a consideration of causes, not much comment is necessary; the degree of patchiness is obvious. What moral can be drawn from it? Let us suppose we had been carrying out a survey in this region using similar nets towed for 10 minutes at points say 10 miles apart; it is clear that we should arrive at very different conclusions as to the distribution of the macroplankton according to exactly where our stations were placed within a circle having a radius of only half a mile. In the consecutive series here described a mile covers three adjacent samples; we see what a contrast there is within any such three we may select. On the evidence provided by this and the only available similar experiments it appears that much of the quantitative plankton distribution work of the past cannot have the degree of validity often attributed to it. Ecological experiments in the field call for a control just as much as those in the laboratory. Each tow-net survey is really in the nature of an experiment; in the case just imagined the experiment was to sample the water at 10 mile intervals to find out the distribution of the more important plankton animals over the area. Before accepting the results as valid a control experiment is necessary to see, if such samples are repeated at several points near the same place, that they give a reasonably consistent result: to see in fact if one such net towed at one place can be said to give a fair measure of the plankton lying to five miles on either side of it.

I once heard quite a well known planktologist say that it did not do to arrange your stations in a survey too close together because it made it almost impossible to use contour methods when charting the results; I don't think he realized the significance of what he was saying.

I gratefully acknowledge the assistance of Dr. C. CHENG in the identification and estimation of the copepods in these samples.

REFERENCES

HARDY, A. C. (1936 A), The Continuous Plankton Recorder. *Discovery Reports*, **11**, 457–510.

HARDY, A. C. (1936 B), Observations on the Uneven Distribution of Oceanic Plankton. *Discovery Reports*, **11**, 513–538.

HARDY, A. C. and GUNTHER, E. R. (1935), The Plankton of the South Georgia Whaling Grounds and Adjacent Waters. *Discovery Reports*, **11**, 1–456.

KEMP, S. and HARDY, A. C. (1929), The *Discovery* Investigations, Objects, Equipment and Methods. Part II. *Discovery Reports*, **1**, 151–222.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 12-14.

Dissolved organic matter in the sea*

By Mary Alys Plunkett† and Norris W. Rakestraw
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We have little real information about the nature and amount of dissolved organic matter in the sea, especially in deep water. Among the few recorded determinations of dissolved organic carbon the limited number made by Krogh (1934) have seemed to us to be perhaps the most reliable. We are but slightly better off in our knowledge about dissolved organic nitrogen. In addition to a few determinations made by Krogh (1934), some results reported by von Brand and Rakestraw (1941), using the same methods, may perhaps be regarded with confidence. On the basis of these limited data it would appear that the concentration of dissolved organic matter in the open sea is fairly constant at about 5 mg per litre.

Krogh's work, just referred to, was carried out with the extreme care and attention to detail which was characteristic of all his microchemical analyses, but because of its limited extent (his carbon results were obtained from six samples collected from a single station) it has long seemed to us highly necessary to corroborate and extend it. His methods have never been used again until very recently, when Kay (1954) used a modification to obtain results in the shallow waters of the Kielerbucht.

Accordingly, in the spring of 1953, we assembled apparatus essentially similar to Krogh's and carried out the analyses shown in Table I, on samples from three stations off the coast of Southern and Lower California. The results are shown graphically in Figure 1, along with curves for temperature and for oxygen at Station 110.70. Two important conclusions emerge:

The general level of concentration of dissolved organic carbon which Krogh reported (two to three milligrams per litre) was confirmed at these stations. However, instead of being homogeneously distributed it is definitely less at intermediate depths. The significance of this fact is not clear; the data are too limited to conclude that it is related to the location of the oxygen-poor layer. In any event, it throws some doubt upon certain of Krogh's conclusions.

In the fall of 1953, samples were obtained from two stations on the " Transpac " expedition in the north-western Pacific. The results from these are tabulated in Table II and graphically shown in Fig. 1. It will be seen that these are rather more irregular in the upper layers and that the general level of concentration is distinctly lower than at the earlier stations. All samples except that from 506 m at Station T-P 99 were analyzed in duplicate. The samples from these two stations were frozen immediately and kept in this condition until analyzed several months later. While this introduces some uncertainty it nevertheless seems unlikely that significant oxidation took place in the meantime. Deep-sea water has been preserved for much longer times and at higher temperatures without appreciable consumption of oxygen (Rakestraw 1947). Keys, Christensen and Krogh (1935) have also shown that the dissolved organic

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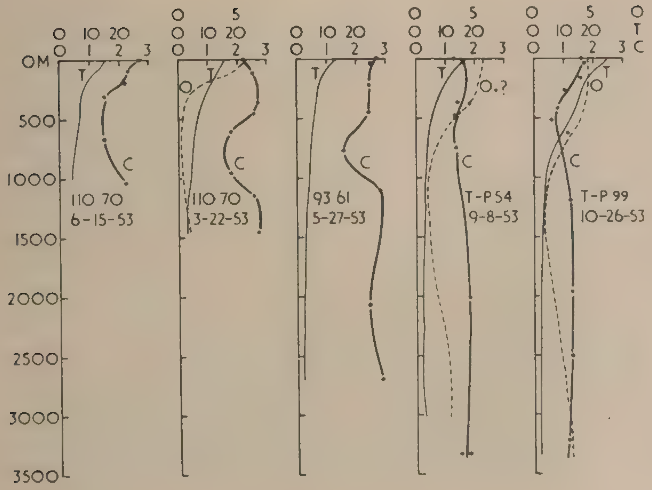

Fig. 1. Vertical distribution of dissolved organic carbon at two stations off the California coast (110.70 and 93.61) and two in the north-western Pacific (T-P 54 and T-P 99). Curves show carbon in mg/L (C), temperature ° C (T) and dissolved oxygen ml/*L* (O).

Table I.—Vertical distribution of dissolved organic carbon

Station	*Location*	*Date*	*Depth (m)*	*Carbon (mg/L)*	*Temp. ° C*	*Dissolved oxygen (ml/L)*
110.70	28° 40′ N 118° 20′ W	6/15/53	0	2·68	16·14	
			99	2·30	13·51	
			195	2·20	9·65	
			317	1·50	8·16	
			665	1·49	5·55	
			1043	2·27	3·93	
110.70	,,	3/22/53	0	2·14	15·62	5·53
			104	2·58	13·96	5·17
			381	2·73	7·78	0·72
			470	2·59	6·90	0·43
			566	1·92	6·22	0·33
			759	1·41	5·09	0·32
			955	1·71	4·23	0·52
			1147	2·58	3·66	0·74
			1487	2·73	2·96	1·10
93.61	32° 50′ N 119° 45′ W	5/27/53	0	2·67	14·36	
			32	2·48	12·94	
			235	2·43	7·73	
			446	2·49	6·12	
			767	1·52	4·59	
			1092	2·76	3·69	
			2077	2·31	2·02	
			2690	2·82	1·73	
100.90	29° 45′ N 120° 50′ W	4/28/53	3000	2·50	—	

matter is very resistant to bacterial action and does not change significantly during storage of water.

We are unable to find any other systematic analytical error which would account for such a large difference in the average concentration in the deep water. On the other hand, it is difficult to explain such a difference, since the phosphate concentration, for example, is approximately the same in the regions concerned. The dissolved organic carbon, although in lower concentration at all depths, is not uniformly distributed vertically, being less in the intermediate zone, as it was in the eastern Pacific. In this case, however, the zone of lower carbon concentration seems to be somewhat above the steep oxygen gradient.

It is important that we learn more about the dissolved organic matter, since it is the largest fraction of the total organic matter in the sea. Although for the most part it seems to be resistant and unreactive we do not know what relation it has to the " oxidizable organic matter " which plays an important part in the distribution of dissolved oxygen. The work reported here will be continued and extended.

Table II.—Vertical distribution of dissolved organic carbon

Station	*Location*	*Date*	*Depth (m)*	*Carbon (mg/L)*	*Temp. (° C)*	*Dissolved oxygen (ml/L)*
T-P 54	40° 34′ N 170° 2′ E	9/8/53	0	1·29	19·2	5·67
			10	1·66	19·0	5·34
			273	2·72	8·9	4·94
			366	1·42	7·0	4·56
			371	1·87	7·0	4·54
			464	1·47	5·8	3·70
			469	1·34	5·7	3·68
			753	1·37	4·3	1·35
			758	1·37	4·3	1·37
			2020	1·78	2·4	1·87
			3340	1·80	1·9	3·40
			3345	1·48	1·9	3·40
T-P 99	31° 55′ N 142° 12′ E	10/26/53	0	1·57	25·4	4·58
			24	1·72	25·0	4·56
			153	1·57	19·2	4·41
			257	1·03	17·1	4·61
			406	0·78	15·3	4·21
			506	0·59	12·9	3·96
			607	1·18	10·3	3·65
			803	0·88	6·3	2·24
			1190	1·27	3·7	0·94
			1995	1·27	2·3	1·76
			2504	1·27	2·1	2·34
			3220	1·12	1·9	3·03
			4177	1·08	1·9	3·44
			5254	0·98	1·9	3·67
			6290	1·18	1·9	3·71

REFERENCES

KAY, H. (1954), Untersuchungen zur Menge und Verteilung der organischen Substanz im Meerwasser. *Kieler Meeresforschungen*, **10**, 202–214.

KEYS, A., CHRISTENSEN, E. H. and KROGH, A. (1935), The organic metabolism of sea water with special reference to the ultimate food cycle in the sea. *J. Mar. Biol. Assn. U.K.*, **20**, 181–196.

KROGH, A. (1934), Conditions of life at great depths in the ocean. *Ecol. Mongr.*, **4**, 430–439.

RAKESTRAW, N. W. (1947), Oxygen consumption in sea water over long periods. *J. Mar. Res.*, **6** (3), 259–263.

VON BRAND, T. and RAKESTRAW, N. W. (1941), The determination of dissolved organic nitrogen in sea water. *J. Mar. Res.*, **4** (1), 76–80.

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Marine bacteria

Recollections and problems

By Selman A. Waksman
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Early in the spring of 1931 I received a telephone call from the venerable biologist, Professor Edwin Conklin of Princeton University, to the effect that Professor Henry Bigelow of Harvard was visiting him that day. They were discussing organizational plans for the newly established Oceanographic Institution at Woods Hole, Mass. The question had come up as to whether it would be desirable to establish a project in marine bacteriology at the Institution. Would I care to come to Princeton and present my ideas concerning the potentialities in this field of research?

I could lay claim to only very limited knowledge of marine bacteria. What little knowledge I had was based on a certain familiarity with a few problems in which marine bacteria were involved. One of these was concerned with precipitation of lime in sea-water. Just prior to World War I, a British bacteriologist, Dr. G. H. Drew, made a study of the precipitation of lime in tropical and subtropical water, notably in the region of the Bahamas. Drew reported this process to be a result of bacterial action. Certain groups of bacteria concerned with the reduction of nitrate to atmospheric nitrogen, or the so-called " denitrifying " types, were said to be primarily involved in the process. The untimely death of Dr. Drew in 1913 brought an end to these investigations.

Seven or eight years later, Professor Charles Lipman of the University of California became interested in this problem. Together with an assistant, he spent two or three summers in the laboratory of the Dry Tortugas, in an attempt to confirm Drews' results. Prof. Lipman visited me on several occasions and we had an opportunity to discuss this problem in detail. It appeared to me that the final answer had not been reached, certainly not as regards the role of bacteria in the process.

In 1929, a group of geologists from Princeton, headed by Professor Richard M. Field, organized an expedition to the Bahamas, particularly Andros Island, for the purpose of studying in detail this precipitation problem. Since " drewite ", the name given to the lime formation, was believed to be of bacteriological origin, it was felt that it would be desirable to have a bacteriologist participate. I was invited, but declined, because neither my available time nor my scientific interests, I felt, would permit me to do justice to the study. I was at that time on the point of developing a comprehensive study of " organic matter decomposition by micro-organisms and of humus formation ", and could not, therefore, afford to undertake a new problem that would require at least several months of my time. The Princeton group decided to invite a qualified bacteriologist interested in this problem. On my part, I promised to make facilities available in my laboratory for this study.

In 1930, Dr. W. Bavendamm, a German bacteriologist, came to this country to spend six months working on this problem. He was immediately placed in our laboratory, where he was supplied with the necessary glassware and chemicals. We also helped to equip him with all the other materials required for the bacteriological phase of the expedition and discussed various aspects of the problem and the methods of approach. It was decided to limit the field expedition to the collection of samples and to carry out the studies themselves in our laboratory. Upon his return from the expedition, Dr. Bavendamm began to examine bacteriologically the samples of sea-water and sea bottom material.

Upon studying the data, I was struck by the frequent occurrence of a certain kind of bacterium which brought about rapid liquefaction of the agar in the medium. Each colony of this bacterium was surrounded by a clear, saucer-like circle of the liquefied agar. Because of my interest in organic matter disintegration, including such compounds as hemicelluloses and polyuronides, of which agar was a type, I suggested to Bavendamm that we both undertake a detailed study of this bacterium and its mode of action upon the agar. He agreed, and the remaining months of his stay in my laboratory were devoted to this investigation. Our results were incorporated in a joint paper, which was submitted to the Journal of Bacteriology, and Bavendamm himself published a paper on the question of calcium precipitation.

It was just about this time that the Oceanographic Institution was being organized. The director, Dr. Henry Bigelow, was approached by Dr. Field, who was requesting support for another expedition to the Bahamas. When asked about the accomplishments of the first expedition, Dr. Field cited the above two papers. When Dr. Conklin's opinion was asked about this matter, he suggested that I be consulted. Hence the telephone call to which I have referred.

There was another reason for consulting me on this matter. Since any comprehensive survey of the field of marine bacteriology would involve an understanding not only of bacteriological processes but of complex bacterial or even microbial populations, a prior knowledge of other complex populations would be helpful. Inasmuch as my own field of study, that of soil microbiology, involved populations and relationships, there was a parallelism between the two. This could be contrasted to medical and industrial microbiology, where single cultures of organisms are concerned. Further, the cycles of life in both the soil and the sea are similar, both as regards the activities of various specific groups of micro-organisms, such as nitrifying, denitrifying, and cellulose-decomposing types, and the bacterial population of the natural substrate as a whole.

We spent several hours that beautiful spring afternoon in Princeton, in 1931, discussing various problems bearing upon marine bacteriology. All three of us reached the conclusion that neither oceanography nor marine bacteriology would gain much from another expedition to the Bahamas. However, we all felt strongly that a definite place on the research program of the Oceanographic Institution should be given to bacteriological investigators. Dr. Bigelow then suggested that I present a tentative plan for such a program. Within a few weeks I submitted a plan based on the idea that one or two investigators interested in complex microbiological activities be invited to spend two or more months every summer at the Oceanographic Institution. A laboratory was to be set aside for this purpose, and several assistants assigned to the project. Further, the senior investigator would continue during the rest of the year to work on one of the problems in his own laboratory, assisted by one or more graduate students provided by the Oceanographic Institution.

My plan was accepted by the Trustees of the Institution, and I was invited to spend a month that summer at Woods Hole to study the situation a little more closely. Subsequently, I was appointed investigator to organize the work in marine bacteriology.

The next 10 years found me busy every summer for about two months at the Oceanographic Institution, searching for bacteria in the sea. There were always several collaborators, assistants, and graduate students to help in the research program. It is of particular interest to mention among the associates Dr. CORNELIA CAREY, Professor of Bacteriology at Barnard, Dr. MARGARET HOTCHKISS of New York Medical College, and, later, Dr. AUSTIN PHELPS of Yale University. Among the assistants who should be mentioned are, first, HERBERT W. REUSZER, CHARLES RENN, J. STOKES, and D. Q. ANDERSON, and, later, CHARLES WEISS, DONALD REYNOLDS, and DON JOHNSTONE. There were also various visiting investigators concerned with microbiological problems, principally Prof. H. GRAN of Oslo, Norway, who has left his mark in bacteriology with his classical study of the agar-liquefying bacteria; Dr. FREDERICK K. SPARROW, who made a study of the fungi in the sea, especially those pathogenic to marine algae; and Prof. U. VARTIOVAARA of Finland. A number of summer laboratory assistants, especially ERIC WARBASSE, contributed much in collecting equipment, for both inside and outside (or boat) work, and helping to organize the laboratory at the Institution.

By the time I started the first investigation in 1931, the laboratories were fully equipped and ready to operate, thanks to the efforts of REUSZER, who did a great deal of the preparatory work, especially prior to my arrival at Woods Hole. He also continued some of the experimental studies in New Brunswick during the rest of the year. It was not until 1932, however, that our program of marine research was fully developed. During the preparatory period I had full opportunity to familiarize myself with the literature on the subject. We decided to approach the study of marine bacteria along four distinct lines:

1. The nature of the bacterial population as a whole, both in sea-water and in the sea bottom. Special attention was given to the influence of distance from land, depth of water, and nature of bottom material. A comparative study was also undertaken of the methods to be used, including suitable media, and of the changes in the population after the samples were taken, especially upon standing in the laboratory. Although most of these studies were quantitative in nature, others were also qualitative, since they involved a study of the specific nature of marine bacteria, such as aerobic *vs.* anaerobic, and spore-forming *vs.* non-spore-forming types.

2. The specific nature of some of the marine bacteria. Particular attention was paid to those responsible for the formation of nitrite and nitrate by oxidation of ammonia, the reduction of nitrate, the fixation of nitrogen, the decomposition of cellulose, and the nature and decomposition of marine algal constituents.

3. Transformation of organic matter in the water and in the bottom material. This included a variety of reactions, such as oxygen consumption, carbon dioxide liberation, and nitrogen transformation. The water from warm regions showed, for example, a higher bacterial population with much less oxygen consumption than did the water from cold regions, when samples of water were kept under identical conditions for equal periods of time. This pointed to a greater concentration of available organic matter in the colder waters.

4. Various other problems came up for consideration during these years. The most important were the following:

(a) A study of the agents responsible for the disappearance of eel-grass along the Atlantic shore. RENN, who was appointed the senior assistant in marine bacteriology after the resignation of REUSZER, undertook this task and made a notable scientific contribution to it.

(b) A study of the presence or development in the sea of bacteria antagonistic or destructive to other bacteria. These particular investigations came toward the end of my stay in Woods Hole, in 1941 and 1942, and were influenced largely by my major interests at Rutgers on the antagonistic interrelations among micro-organisms and the production of antibiotic substances.

(c) The role of bacteria in the fouling of ship bottoms. This problem also came toward the end of my work at Woods Hole and on the eve of World War II. Since the chemists and biologists of the Institution soon took over this problem, it will no doubt be reported in this volume in further detail.

In addition to my work in the laboratory at the Oceanographic Institute, limited periods were spent elsewhere in connection with some of the marine microbiological problems. It is sufficient to mention two brief stays at the Bermuda Biological Station, and various trips on the ocean-going laboratory vessels, such as the *Atlantis*. The first were successful, since I had a first-hand opportunity to compare the bacterial population and the bacteriological changes in the waters in a warm region with those of cold regions. The ocean trips, however, were a complete failure, so far as I was concerned. Under the threefold movements of the ship, I immediately became seasick and had to leave the work largely to one of the assistants who always accompanied me. After two valiant efforts to carry out studies on the moving boat, I made no further attempts. Dr. BIGELOW's comment, " Food was wasted on him ", was fully justified, and I gave up further sea voyages for bacteriological exploration. Fortunately, some of the assistants, especially RENN, REYNOLDS, and JOHNSTONE, were excellent sailors, and could take good care of the problems under consideration.

Thus came to an end a decade of exploration of the sea for marine bacteria. The following list of papers published from the Oceanographic Institution bears evidence of the scope of the subject, the variety of problems involved, and some of the results attained. It affords proof of the vision and far-sightedness of the founder of the Oceanographic Institution and its first Director, Dr. HENRY BIGELOW, to whom this note is gratefully dedicated.

REFERENCES

Preliminary papers:

BAVENDAMM, W. (1931), The possible role of micro-organisms in the precipitation of calcium carbonate in tropical seas. *Science*, **73**, 597–598.

BAVENDAMM, W. (1932), Die mikrobiologische Kalkfällung in der tropischen See. Bericht über die mikrobiologischen Ergebnisse einer in Jahre 1930 von der Universitäten Princeton und Rutgers (U.S.A.) unternommenen Forschungsreise nach den Bahama-Inseln. *Arch. Mikrobiol.*, 3, 205 276.

WAKSMAN, S. A. and BAVENDAMM, W. (1931), On the decomposition of agar-agar by an aerobic bacterium. *J. Bacteriol.*, **22**, 91–102.

Published papers from the Woods Hole Oceanographic Institution:

ANDERSON, D. Q. (1940), Distribution of organic matter in marine sediments and its availability to further decomposition. *J. Mar. Res.*, **2**, 225–235.

CAREY, C. L. (1938), The occurrence and distribution of nitrifying bacteria in the sea. *J. Mar. Res.*, **1**, 291–304.

CAREY, C. L. and WAKSMAN, S. A. (1934), The presence of nitrifying bacteria in deep seas. *Science*, **79**, 349–350.

HOCK, C. W. (1940), Decomposition of chitin by marine bacteria. *Biol. Bull.*, **79**, 199–206.

HOCK, C. W. (1941), Marine chitin-decomposing bacteria. *J. Mar. Res.*, **4**, 99–106.

HOTCHKISS, M. and WAKSMAN, S. A. (1936), Correlative studies of microscopic and plate methods for evaluating the bacterial population of the sea. *J. Bacteriol.*, **32**, 423–432.

RENN, C. E. (1934), Wasting disease of *Zostera* in American waters. *Nature*, **134**, 416–417.

RENN, C. E. (1935), A mycetozoan parasite of *Zostera marina*. *Nature*, **134**, 544–545.

RENN, C. E. (1936), The wasting disease of *Zostera marina*. I. A phytological investigation of the diseased plant. *Biol. Bull.*, **70**, 148–158.

REUSZER, H. W. (1933), Marine bacteria and their role in the cycle of life in the sea. III. The distribution of bacteria in the ocean water and muds about Cape Cod. *Biol. Bull.*, **65**, 480–497.

WAKSMAN, S. A. (1933), On the distribution of organic matter in the sea bottom and the chemical nature and origin of marine humus. *Soil Sci.*, **36**, 125–147.

WAKSMAN, S. A. (1934), The role of bacteria in the cycle of life in the sea. *Sci. Monthly*, **38**, 35–49.

WAKSMAN, S. A. (1934), The distribution and conditions of existence of bacteria in the sea. *Ecol. Monogr.*, **4**, 523–529.

WAKSMAN, S. A. (1941), Aquatic bacteria in relation to the cycle of organic matter in lakes. A Symposium on Hydrobiology, Madison, Wisconsin, 86–105.

WAKSMAN, S. A. and CAREY, C. L. (1933), Role of bacteria in decomposition of plant and animal residues in the ocean. *Proc. Soc. Exp. Biol. Med.*, **30**, 526–527.

WAKSMAN, S. A. and CAREY, C. L. (1935), Decomposition of organic matter in sea water by bacteria. I. Bacteria multiplication in stored sea water. *J. Bacteriol.*, **29**, 531–543.

WAKSMAN, S. A., CAREY, C. L. and ALLEN, M. C. (1934), Bacteria decomposing alginic acid. *J. Bacteriol.*, **28**, 213–220.

WAKSMAN, S. A., CAREY, C. L. and REUSZER, H. W. (1933), Marine bacteria and their role in the cycle of life in the sea. *Biol. Bull.*, **65**, 57–79.

WAKSMAN, S. A. and HOTCHKISS, M. (1937), Viability of bacteria in sea water. *J. Bacteriol.*, **33**, 389–400.

WAKSMAN, S. A. and HOTCHKISS, M. (1938), On the oxidation of organic matter in marine sediments by bacteria. *J. Mar. Res.*, **1**, 101–118.

WAKSMAN, S. A. HOTCHKISS, M. and CAREY, C. L. (1933), Marine bacteria and their role in the cycle of life in the sea. II. Bacteria concerned in the cycle of nitrogen in the sea. *Biol. Bull.*, **65**, 137–167.

WAKSMAN, S. A., HOTCHKISS, M., CAREY, C. L. and HARDMAN, YVETTE (1938), Decomposition of nitrogenous substances in sea water by bacteria. *J. Bacteriol.*, **35**, 477–486.

WAKSMAN, S. A., and RENN, C. E. (1936), Decomposition of organic matter in sea water by bacteria. III. Factors influencing the rate of decomposition. *Biol. Bull.*, **70**, 472–483.

WAKSMAN, S. A., REUSZER, H. W., CAREY, C. L., HOTCHKISS, M. and RENN, C. E. (1933), Studies on the biology and chemistry of the Gulf of Maine. III. Bacteriological investigations of the sea water and marine bottoms. *Biol. Bull.*, **65**, 183–205.

WAKSMAN, S. A., STOKES, J. L. and BUTLER, M. R. (1937), Relation of bacteria to diatoms in sea water. *J. Mar. Biol. Assoc.*, U.K., n.s., **22**, 359–373.

WAKSMAN, S. A. and VARTIOVAARA, UNTO (1938), The adsorption of bacteria by marine bottom. *Biol. Bull.*, **74**, 56–63.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 20-.39

The strontium-calcium atom ratio in carbonate-secreting marine organisms

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Summary—The purpose of the present investigation was to study the distribution of strontium and calcium in the biosphere. The contents of strontium and calcium in 250 species of carbonate-secreting marine organisms were determined. The strontium-calcium atom ratio in calcareous portions of marine organisms ranged from $1{\cdot}0$ to 11×10^{-3}. With the exception of Nudibranchia and Madreporaria, the atom ratio in marine organisms was less than that of sea water, $8{\cdot}9 \times 10^{-3}$. The strontium-calcium atom ratios in marine organisms appeared to be constant in accordance with their phylogenetic classification. Specimens of different species collected from a common ecological community showed diverse strontium-calcium atom ratios. On the other hand, the similar types of marine organisms living under different environmental conditions from arctic to tropical oceans, showed constant strontium-calcium atom ratios. Variations in salinity and temperature of sea water were apparently not the factors which influenced the strontium-calcium atom ratio in calcareous shells.

The mineralogical properties of calcium carbonate in marine organisms demonstrated a definite correlation with the occurrence of strontium. The marine organisms containing calcium carbonate as aragonite had strontium-calcium atom ratios greater than those as calcite. Samples of deep-sea sediments and *Clobigerina* ooze showed strontium-calcium atom ratios of $1{\cdot}94 \times 10^{-3}$ and $1{\cdot}49 \times 10^{-3}$, respectively. The limestone deposits, which originated from marine organisms, had the smallest strontium-calcium atom ratio, $0{\cdot}63 \times 10^{-3}$, of all materials examined. Apparently, the matrix of calcareous deposits of marine origin has lost strontium during geological time.

INTRODUCTION

THE PRESENT investigation was undertaken in order to study (1) the distribution of strontium in the carbonate-secreting marine organisms, (2) to ascertain possible correlations between the strontium and calcium contents of the calcareous skeletons, (3) to observe variations of the strontium-calcium atom ratio in accordance with the phylogeny of the marine organisms, (4) to note the extent of change in the atom ratio of marine organisms living in different natural environments, and (5) to determine the strontium content in relation to the mineralogical character of the calcium carbonate in the organisms.

The determination of small quantities of strontium in the presence of large amounts of calcium has been rather a laborious process. However, both of these elements can be determined readily by flame photometric methods recently described by CHOW and THOMPSON (1955 A and B).

REVIEW OF LITERATURE

The occurrence of calcium in marine organisms has been studied extensively, as it is the major constituent of many skeletal remains in calcareous marine sediments. An authoritative summary and discussion on the distribution of calcium in marine organisms has been presented by VINOGRADOV (1953). The investigations of LOWEN-

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STAM (1954 A and B) dealt with the effect of environmental factors upon the mineralogical character of the calcium carbonate in certain marine organisms.

Strontium has been detected in all phases of the biosphere. Due to the difficulty in analyzing trace quantities of strontium in the presence of calcium, only a few scattered analyses were reported in the early literature showing the existence of strontium in marine organisms (MORETTI, 1813; VOGEL, 1814; FORCHHAMMER, 1852; DIEULAFAIT, 1877; SCHMELCK, 1901). More recently, the role of strontium in the carbonate-secreting marine organisms has been the object of investigation, and several quantitative determinations were made on the distribution of strontium in various biological materials (FOX and RAMAGE, 1931; NOLL, 1934; MCCANCE and MASTERS, 1937; WEBB, 1937; TRUEMAN, 1944; TSUCHIYA, 1944, 1948; VINOGRADOV and BOROVIK-ROMANOVA, 1945; ASARI, 1950; ODUM, 1951 A). The relationship between the strontium content of fossils and that of recent marine organisms has also been studied (ODUM, 1951 B; KULP, *et al.*, 1952).

In summarizing the work of previous investigators, it may be said that strontium was found not only in the calcareous shells, but also in the tissues of marine organisms. It was also stated by some that the primary factor which determines the strontium-calcium atom ratio in the calcareous skeletons is the atom ratio of these elements occurring in the water in which the organisms lived. Experiments showed that large quantities of strontium could be taken into the calcareous shells of marine organisms grown under controlled conditions and that the relationship between the strontium-calcium atom ratio in the shells is almost directly proportional to the atom ratio of the environment. Since the strontium-calcium atom ratio in the calcareous skeletons reflects the chemical composition of the water, the analysis of the strontium-calcium atom ratio in unaltered fossils could be used as a valid method of measuring the strontium-calcium ratio of the ancient oceans. Such findings presented strong evidence that the strontium-calcium atom ratio of ocean waters has been of about the same order of magnitude since Palaeozoic times at least, because this atom ratio of the fossils resembles that of the modern counterparts.

In marine organisms the strontium-calcium atom ratio of the growing shells is apparently independent of the age of the organisms. No evidence was found that would indicate any seasonal fluctuations in the strontium-calcium atom ratio of marine organisms. It was also concluded that the temperature of the ocean waters is a relatively insignificant factor in affecting the strontium content of marine organisms.

Besides the chemical composition and the ecological environment, the mineralogical character, such as crystal lattice, of the calcareous skeletons was of some significance. It was found that there is always more strontium present when the calcium carbonate exists as aragonite rather than as calcite.

METHODS OF ANALYSIS

All chemicals used in the present investigation were of analytical grade and tested for traces of strontium and calcium. A stock solution of strontium, 6·00 mg-atoms per litre, was prepared by dissolving 0·886 gram of strontium carbonate in a limited volume of hydrochloric acid and then diluting to one litre; and that of calcium, 20·0 mg-atoms per litre, was prepared by dissolving 2·002 grams of calcium carbonate in hydrochloric acid and diluting to one litre. From such stock solutions, suitable aliquots were taken and diluted for the comparison standards. Polyethylene containers were used for storage of standard solutions in order to avoid possible contamination from the glassware.

The calcareous skeletons of the marine organisms were carefully cleaned and air-dried. Duplicate weighed samples (0·5 to 1·0 gram) of the dried materials were heated in an oven to a temperature of 350° C and then cooled. The loss in weight was designated as the organic matter. The samples were then further ignited at 1,100° C until all carbonates were decomposed. Upon cooling and weighing, the difference in weight was considered as carbon dioxide. The residues were treated with 10 ml of water, and 12 N hydrochloric acid was added dropwise until solution was complete. The solutions were then diluted to one litre, thoroughly mixed, and analyzed for strontium and calcium using the "internal standards" technique of flame photometry by CHOW and THOMPSON (1955 A and B).

RESULTS OF ANALYSIS

All analyses were made on the fresh calcareous skeletons (unless otherwise stated) which had been carefully cleaned and air-dried for several weeks. In order to obtain a general idea of the distribution of strontium in the biosphere, a large variety of species of carbonate-secreting marine organisms was analyzed, rather than concentrating on possible variations in just a few particular species.

In tables the calcium, strontium, carbon dioxide and organic matter content of the organisms are reported as percent of constituents in air-dried samples. To demonstrate more clearly the relation of the strontium to the calcium, it was deemed desirable to report this relationship as the atom ratio of strontium to calcium. For example, the calcareous alga, *Bossea orbigniana*, contains 0·199% of strontium and 29·2% of calcium. The strontium-calcium atom ratio would be:

$$\frac{0{\cdot}199/87{\cdot}63}{29{\cdot}2/40{\cdot}08} = 3{\cdot}12 \times 10^{-3}$$

and indicates that for every 1,000 atoms of calcium there are present approximately three atoms of strontium.

The mineralogical data cited in this paper were taken from the publications of BØGGILD (1930), VINOGRADOV (1953) and CHAVE (1954). However, the mineralogical properties of the specimens, which were analyzed chemically by the authors, will be studied further by Dr. R. G. BADER.

DISCUSSION

Phylogenetic Aspects:

1. *Marine Algae:* In most of the previous studies on calcareous algae, determinations of calcium and magnesium were given, the calcium carbonate in the skeletons being reported as calcite. Only one analysis of strontium was reported, which showed 0·26% of strontium in the ash of *Lithothamnion polymorphum* (NOLL, 1934).

The results of analysis of calcareous algae, Corallinaceae, are shown in Table I(A). The average strontium-calcium atom ratio was $3{\cdot}20 \times 10^{-3}$. The diatoms, *Coscinodiscus*, were also analyzed. As they are primarily of a silicious nature, only traces of calcium were found in the skeletons.

2. *Phylum Protozoa:* The calcium content of Foraminifera has been investigated extensively, especially its relation to the origin of calcareous marine sediments, but no strontium determinations appeared in the literature.

Analyses of calcareous Foraminifera (Table I (B)) by the authors showed an average strontium-calcium atom ratio of $3{\cdot}07 \times 10^{-3}$. The presence of magnesium in the skeletons was detected qualitatively. It has long been known that radiolarian skeletons are rich in strontium, but the authors were unable to collect sufficient material for a quantitative study.

3. *Phylum Porifera:* The classification of sponges is based on the chemical composition of the skeletons such as the Calcarea containing calcite spicules. FOX and RAMAGE (1931) noted the presence of strontium in Porifera when they examined the ash of *Clathrina* spectroscopically.

The average strontium-calcium atom ratio of calcareous sponges, Calcarea, containing measurable quantities of strontium, was 2·99 × 10^{-3} (Table I (C)). The calcium content in silicious sponges, Demospongiae, was minute; only traces of strontium were detected.

4. *Coelenterata:* The high strontium content in corals was observed by NOLL (1934). He reported the following results as percentage of strontium in their ash: hydrozoan *Millepora alcicornis*, 0·43%; alcyonarian *Corallium rubrum*, 0·17%; and madreporarian *Porites clavaria*, 0·42%. ODUM (1951 B) reported an average strontium-calcium atom ratio of 10·6 × 10^{-3} for corals. The calcium carbonate of Hydrozoa and Madreporaria was reported as aragonite, whereas that of Alcyonaria was calcite.

In Table I (D) are the results of analysis on calcareous portions of Coelenterata. In Hydrozoa, the Hydrocorallina possess calcareous skeletons. Except *Errinopora zarhyncha*, all the analyses yielded high strontium-calcium atom ratios which averaged 9·49 × 10^{-3}.

The soft corals, Alcyonaria, contained less strontium than other corals, and magnesium was present in the skeletons. However, *Heliopora coerulea*, which has the calcium carbonate in the form of aragonite, showed a much higher atom ratio than other Alcyonaria. The *Heliopora* with their external tube-like skeletons differ morphologically from all other Alcyonaria. With the high content of organic matter and their strontium-calcium atom ratios comparable to Porifera (Calcarea), it is interesting to note that the skeletons of Alcyonaria also have much in common morphologically with those of Porifera.

The solitary corals, Madreporaria, were found to have consistently high strontium-calcium atom ratios with an average of 9·86 × 10^{-3}. This is one of the orders of marine organisms to show the atom ratio equal to or greater than that of sea water, 8·9 × 10^{-3}.

5. *Minor Phyla:* Specimens of these skeletonless marine organisms were analyzed. They were *Bolinopsis microptera* (Ctenophora), *Notoplana acticola* (Platyhelminthes), *Micrura verrilli* (Nemertea), *Urechis caupo* (Echiuroidea), *Phascolosoma agassizii* (Sipunculoidea), and *Phoronopsis viridis* (Phoronidea). Being non-carbonate secreting, these organisms contained 85 to 99% of organic matter which varied considerably among specimens. Calcium was always present in the ash of the organisms, and only traces of strontium could be detected.

6. *Phylum Annelida:* Many members of Annelida such as Polychaeta possess calcareous tubes which serve to shelter them. LOWENSTAM (1954 A) reported from 0·2 to 0·9% of strontium in the calcareous tubes of Serpulidae. CHAVE (1954) showed that the calcium carbonate in Polychaeta varies from pure calcite in specimens collected in the north Pacific and Behring Sea to almost pure aragonite in specimens collected in tropic areas.

Analyses of calcareous annelid tubes given in Table I (E) showed strontium-calcium atom ratios ranging from 3·86 to 8·22 × 10^{-3}. This is the only group of marine organisms that demonstrated a wide range for the strontium-calcium atom ratio.

7. *Phylum Arthropoda:* The Arthropoda are represented in the ocean mainly by species of Crustacea. The majority of Crustacea possesses chitinous exoskeletons. The Cirripedia is the only group in this phylum which possesses calcareous skeletons

of calcite structure. Besides the Cirripedia, the Decapoda also contain calcite as well as an appreciable amount of phosphorite. VINOGRADOV and BOROVIK-ROMANOVA (1945) found 0·2% of strontium in the ash of *Balanus balanoides*. WEBB (1937) also reported 0·1% of strontium in the ash of the hermit crab *Eupagurus* (=*Pagurus*) *bernhardus*.

The results of analysis of calcareous portions of Arthropoda are given in Table I (F). The strontium-calcium atom ratios of Cirripedia averaged 4·45 × 10^{-3}, which is the highest value for the organisms containing calcite.

The canapace of Decapoda was found to contain more organic matter than Cirripedia, but their strontium contents were of the same order of magnitude, although the calcium content of Decapoda was much lower. Appreciable amounts of magnesium and phosphate were detected qualitatively. The strontium-calcium atom ratio was rather uniform with an average of 6·17 × 10^{-3}. The claws of *Cancer antennarius* were also analyzed, and showed no difference in chemical composition as compared to the carapace. The soft carapace of *C. productus* in its moulting stage was found to consist mainly of organic matter and only 0·44% of calcium. This may be cited as an illustration of the change in chemical composition of the exoskeletons during moulting.

8. *Phylum Mollusca:* The molluscs are widely distributed in the ocean and constitute the largest invertebrate group which possesses calcareous protective shells. The chemical composition, mainly calcium, of Pelecypoda and Gastropoda was studied by CLARKE and WHEELER (1922), FOX and RAMAGE (1931), NOLL (1934), MCCANCE and MASTERS (1937), WEBB (1937), ASARI (1951), ODUM (1951 B), KULP, *et al.* (1952) and VINOGRADOV (1953). The majority of Pelecypoda and Gastropoda possesses shells consisting chiefly of a calcite-aragonite mixture. Only three families (Anomiidae, Ostreidae and Pectinidae) were reported to have calcite shells. Aragonite was reported in calcareous portions of Amphineura, Scaphopoda, Cephalopoda and Nudibranchia.

Class Amphineura: The chitons are considered morphologically to constitute the most primitive class of living shell-bearing molluscs. Only a few calcium analyses on these organisms were reported and none on strontium.

The results of analysis of chiton plates are given in Table I (G). They were composed mainly of calcium carbonate with relatively high percentage of strontium. The strontium-calcium atom ratios averaged 8·06 × 10^{-3} which was much higher than those in other classes of molluscs.

Class Pelecypoda: The results of analysis of 44 species of Pelecypoda are shown in Table I (H). Nine families (Myidae, Clinocardium, Saxicavidae, Tellinidae, Lyonsiidae, Mactridae, Periplomatidae, Pholadidae and Solenidae) had strontium-calcium atom ratios greater than 2·0 × 10^{-3}. The lowest strontium-calcium atom ratio was found in the families which were reported as having calcite shells, and that of the highest was Myidae.

Class Gastropoda: Forty-six species of subclass Prosobranchia shown in Table I (I) were analyzed. The strontium-calcium atom ratios among all families ranged from 1·31 to 2·14 × 10^{-3} and were less than that for Pelecypoda.

The Nudibranchia of subclass Opisthobranchia do not possess any calcareous protective shells. The body wall of *Anisodoris* and *Archidoris*, which contains calcareous materials, was analyzed (Table I (I)). The organisms were high in organic matter and gave an average strontium-calcium atom ratio of 10×10^{3}. This appears to be in agreement with the finding of McCance and Masters (1937) that *Archidoris britannica* has a high strontium-calcium atom ratio. However, the strontium and calcium content occurs in such low concentrations that a slight experimental error in the determination of either one of the elements markedly affects the atom ratio.

Class Scaphopoda: The analysis of Scaphopoda was performed on *Dentalium* which was reported to have a strontium-calcium atom ratio of $2{\cdot}34 \times 10^{-3}$ (Odum, 1951 b). The specimen of *Dentalium entale* (Table I (J)) analyzed by the authors showed an atom ratio of $2{\cdot}35 \times 10^{-3}$.

Class Cephalopoda: Modern Cephalopoda, except *Nautilus*, usually possess an inner shell. In general, the calcareous inner shells contain more organic matter than the shells of Pelecypoda and Gastropoda. Odum (1951 b) reported a strontium-calcium atom ratio of $3{\cdot}87 \times 10^{-3}$ for a species of *Nautilus*. The inner shell of *Sepia* (Table I (J)) was found by the authors to have an atom ratio of $3{\cdot}74 \times 10^{-3}$. The chitinous plate of *Loligo opalescens* was found to contain chiefly organic matter and traces of calcium.

9. *Phylum Bryozoa:* The calcium content of Bryozoa studied by previous investigators was reported as calcite, but there was little information on the occurrence of other elements. In Table I (K) are the results of analysis of Bryozoa. The strontium-calcium atom ratios averaged $3{\cdot}41 \times 10^{-3}$. An appreciable amount of magnesium was present.

10. *Phylum Brachiopoda:* The calcareous shells of Class Articulata were reported as containing calcite. Odum (1951 b) found a strontium-calcium atom ratio of $1{\cdot}75 \times 10^{-3}$ for a species of *Terebratula*. The other class of Brachiopoda, Inarticulata, consists of apatite, and an atom ratio of $3{\cdot}60 \times 10^{-3}$ was reported for a species of *Crania* (Odum, 1951 b). Analyses by the authors showed that Articulata shells (Table I (L)) had strontium-calcium atom ratios ranging from 1·20 to $1{\cdot}57 \times 10^{-3}$.

11. *Phylum Echinodermata:* With the exception of Holothuroidea, the Echinodermata possess calcium-magnesium skeletons. The body wall of *Psolus* possesses calcareous plates. The calcium carbonate in skeletons was reported as calcite. Previous investigators reported the following results expressed as percentage of strontium in the ash: *Asterias rubens*, 0·8%; *Marthasterias glacialis*, 0·6%; and *Ophiocomina nigra*, 1% (Webb, 1937); *Asterias rubens*, 0·15%; *Gorgonocephalus eucnemis*, 0·2%; *Ophiopholis aculeata*, 0·2%; and *Strongylocentrotus dröbachiensis*, 0·15% (Vinogradov and Borovik-Romanova, 1945).

The results of analysis of calcareous portions of Echinodermata are shown in Table I (M). All five classes of Echinodermata showed remarkable uniformity in the strontium-calcium atom ratio which could be considered as a constant.

12. *Phylum Chordata:* The results of analysis are given in Table I (N). The organisms contained an undetermined amount of sand particles and only traces of strontium.

In Table II are the results of analysis of calcareous materials other than marine invertebrates. The relationship between the strontium-calcium atom ratios of marine Arthropoda and Mollusca and those of fresh water organisms, from the meagre data available for the latter, indicated an analogy: the fresh-water organisms having lower atom ratios.

A summary of all analytical results is presented phylogenetically in Table III. The data given for each column represent the average values obtained on various carbonate-secreting marine organisms as listed in foregoing tables. The strontium-calcium atom ratios are very constant in accordance with the phylogenetic classification. With the exception of Zoantharia (Madreporaria) and Opisthobranchia (Nudibranchia), the atom ratios in calcareous portions of marine organisms are less than that of sea-water, $8{\cdot}9 \times 10^{-3}$. In these instances and in that of radiolaria (ODUM, 1951 A), it is apparent that strontium does play a physiological role in the development of calcareous shells of carbonate-secreting marine organisms. The mechanism of this selectivity presents an interesting physiological problem. Controlled laboratory experiments of growing marine organisms in artificial sea-water free of strontium, and further elaborating ODUM's work with waters of varying strontium-calcium atom ratios, would probably yield fundamental information for explaining the role of strontium in marine organisms.

Ecological Aspects

1. *Habitat:* Organisms of various species are found associated together in an ecological niche. All species that have not adjusted themselves physiologically to the existing conditions will be eliminated from a given community. Since the environmental conditions influence the life of marine organisms, it is of interest to observe any variations of chemical composition of marine organisms which live in such a community. Various species were collected from two rocky shores near the Hopkins Marine Station, California, at the mid and the low inter-tidal levels. The results of analyses of calcareous portions of these organisms are listed in Table IV.

The strontium-calcium atom ratios of the organisms collected at the mid-tidal level varied from $1{\cdot}01 \times 10^{-3}$ (*Mytilus californianus*) to $7{\cdot}91 \times 10^{-3}$ (*Nuttallina californica*). The *Mytilus-Mitella-Pisaster* which were closely associated in the habitat, showed striking differences in the strontium-calcium atom ratio. The organisms collected at the low inter-tidal level had strontium-calcium atom ratios ranging from $1{\cdot}35 \times 10^{-3}$ (*Diodora aspera*) to 11×10^{-3} (*Anisodoris nobilis*). It appears that the marine organisms which live in the same ecological niche accumulate calcium and strontium in their calcareous shells in decidedly different proportions. On the other hand, a very definite relationship between the atom ratio and the phylogenetic classification of the organisms is indicated.

Another series of studies was carried out on the specimens of Echinodermata. Species of Echinodermata which lived in different habitats varying from inter-tidal rocky shore to deep-water, muddy substratum were collected near the Carmel-Monterey-Pacific Grove area. All Echinodermata given in Table V showed a remarkable constancy in their strontium-calcium atom ratios ranging from $2{\cdot}56$ to $2{\cdot}89 \times 10^{-3}$. Allowing for the individual variation and for experimental error, the atom ratios can be considered as identical for the whole phylum. Thus it may be concluded that some types of marine organisms will have a constant strontium-calcium atom ratio in their calcareous skeletons regardless of their habitats.

2. *Water temperature:* The water temperature as well as the salinity affect the solubility of the calcium and strontium carbonates in sea water. WATTENBERG and TIMMERMANN (1936) demonstrated that the solubility of calcium carbonate in sea water increased with increasing salinity and with decreasing temperature. The

strontium and calcium carbonates had identical solubility products of 5×10^{-7} in sea water at a temperature of 20° C and a salinity of $35^{\circ}/_{\circ\circ}$ (Wattenberg and Timmermann, 1938).

Bøggild (1930) stated that ecological variations are not effective on the form of calcium carbonate in marine organisms. Odum (1951 b) and Kulp, *et al.* (1952) have also concluded that the sea water temperature is not an important factor in determining the chemical composition of calcareous skeletons. However, Lowenstam (1954 b) demonstrated that the environmental factors, principally temperature, greatly influence the mineralogical properties of calcium carbonate in some marine organisms.

The data obtained by the authors (see Table I) showed that some types of marine organisms collected from arctic to tropical oceans always consisted of a nearly constant strontium-calcium atom ratio in their calcareous shells regardless of the water temperature of the environment.

3. *Salinity:* In their studies of strontium in fossils and limestones, Kulp, *et al.* (1952) stated that " the primary factor which determines strontium-calcium ratio in the shell or limestone is the strontium-calcium ratio of the water from which these are deposited. The strontium-calcium ratio of the water in turn is related to the salinity and the source." Odum (1951 b), who used artificial sea waters of varying strontium-calcium atom ratios, demonstrated that this ratio in the calcareous shell of *Physa* is directly proportional to that of artificial sea water. He also reported an atom ratio of $9{\cdot}23 \times 10^{-3}$ for the Atlantic Ocean water. Later investigations by Chow and Thompson (1955 a and b) showed that samples of sea water collected from various oceans have a constant ratio between strontium and chlorinity, and calcium and chlorinity. Thus, the strontium-calcium atom ratio would be a constant ($8{\cdot}9 \times 10^{-3}$) regardless of the salinity of ocean waters. From these findings and the experiments of Odum (1951 b), it may be concluded that dilution or concentration of sea water within the tolerance of marine organisms would not be an influential factor on the strontium-calcium atom ratio of calcareous skeletons.

Mineralogical Aspects

Noll (1934) concluded from his investigations that there is always more strontium associated with aragonite limestones than with calcite limestones. Kulp, *et al.* (1952) substantiated this by stating that calcite has a crystal lattice which is less amenable to strontium than the aragonite lattice. Vinogradov (1953) implied that Noll's rule cannot be applied strictly to calcareous shells of marine organisms, but that the rule is valid, in general, for many of them.

The analytical results obtained by the present authors together with the mineralogical data secured by previous investigators are summarized in Table VI. The majority of the specimens studied apparently had calcium carbonate existing as calcite. The calcite group includes Algae (Corallinaceae), Protozoa (Foraminifera), Porifera (Calcarea), Coelenterata (Alcyonaria), Arthropoda (Cirripedia), Mollusca (Anomiidae, Ostreidae and Pectinidae of Pelecypoda), Bryozoa, Brachiopoda (Articulata) and Echinodermata. The average strontium-calcium atom ratio of this group ranged from $1{\cdot}22$ to $4{\cdot}45 \times 10^{-3}$. In phylum Mollusca, the Pelecypoda (except three families mentioned above) and the Gastropoda (Prosobranchia) had a calcite-aragonite mixture in their shells. The strontium-calcium atom ratios of this group were $1{\cdot}94 \times 10^{-3}$ and $1{\cdot}49 \times 10^{-3}$, respectively.

Aragonite was reported only in the calcareous portions of Coelenterata (Hydrozoa and Madreporaria) and Mollusca (Amphineura, Scaphopoda, Cephalopoda and Nudibranchia). The strontium-calcium atom ratios of the aragonite group ranged from 2·35 to 10×10^{-3}. Scaphopoda and Cephalopoda which contain aragonite had atom ratios of $2{\cdot}35 \times 10^{-3}$ and $3{\cdot}74 \times 10^{-3}$, respectively. When comparisons are made mineralogically among molluscs, there is demonstrated a very definite trend for the occurrence of strontium, that is, aragonite Mollusca (10, 8·06, 3·74 and $2{\cdot}35 \times 10^{-3}$), aragonite-calcite mixture Mollusca (1·94 and $1{\cdot}68 \times 10^{-3}$) and calcite Mollusca (1·31 and $1{\cdot}22 \times 10^{-3}$). It appears logical to conclude, therefore, that marine skeletons consisting of aragonite contain more strontium than those of calcite.

The mineralogical structure of calcium carbonate in Polychaeta (Annelida) is not certain. It was reported (Chave, 1954) that species of *Serpula* contained calcium carbonate that varies from pure calcite in one specimen to pure aragonite in another. The Polychaeta shown in Table I (E) had an average strontium-calcium atom ratio of $5{\cdot}86 \times 10^{-3}$, and thus it may be concluded that for most specimens examined, the calcium carbonate is predominantly aragonite.

The Decapoda (Arthropoda), which were found to contain an appreciable amount of phosphorite as well as calcite, showed an average strontium-calcium atom ratio of $6{\cdot}17 \times 10^{-3}$. This is in agreement with Odum's findings (1951 b) on the phosphate in Brachiopoda, and with the statement of Kulp, *et al.* (1952) that the presence of phosphate in the shells tends to yield a high strontium-calcium atom ratio.

Analyses (Table II) on *Globigerina* ooze of the Pacific Ocean which consists mainly of calcium carbonate, showed a strontium-calcium atom ratio of $1{\cdot}49 \times 10^{-3}$. The calcareous deep-sea sediments from the Indian Ocean showed an atom ratio of $1{\cdot}94 \times 10^{-3}$. These values are in marked contrast to those obtained by Kulp, *et al.* (1952) but are in excellent agreement with an average value of $1{\cdot}86 \times 10^{-3}$ given by Odum (1951 b).

The matrix of Permian limestone deposits from Roche Harbour, Washington, showed the lowest strontium-calcium atom ratio, $0{\cdot}63 \times 10^{-3}$, of all materials examined. This finding is comparable to the average atom ratio of $0{\cdot}71 \times 10^{-3}$ on a number of limestone samples obtained by Kulp, *et al.* (1952) and to the value cited by Rankama and Sahama (1949). The matrix of strontionite deposits from Anacortes, Washington, contained 3·56% of calcium and 52·5% of strontium respectively, equivalent to an atom ratio of $6{,}750 \times 10^{-3}$.

Most of the analyses of calcareous portions of living marine organisms showed strontium-calcium atom ratios greater than those obtained on marine sediments. The strontium-calcium atom ratio for these marine sediments in turn was greater than those for the matrix of geologically older limestone deposits of marine origin. Furthermore, calcium carbonate deposited originally as aragonite should contain more strontium than that of calcite, as evidenced by analyses given above. Aragonite limestones are metastable and, in geological time, eventually change into calcite limestones which have a strontium-calcium atom ratio much less than that of marine organisms. Thus it seems logical to conclude that the strontium content of calcareous deposits decreases as the result of geological aging.

To explain the elimination of strontium from calcareous deposits, the following is postulated: the solubility products of calcium and strontium carbonates are about the same order of magnitude, 5×10^{-7}, in sea water at a temperature of 20° C and a salinity of 35°/₀₀ (WATTENBERG and TIMMERMANN, 1938). When marine organisms die and disintegrate, there is a tendency for calcareous materials to halmyrolyze and go into solution. Should strontianite ($SrCO_3$) be present, it would dissolve slowly because sea water is not saturated with respect to strontium carbonate. On the other hand, the ionic strength of calcium in sea water is such that the re-solution of calcium carbonate is exceedingly limited. Should celestite ($SrSO_4$) be present in such marine organisms which have a high strontium-calcium atom ratio, it would leach much more readily from the calcareous matrix, as strontium sulphate is about ten times more soluble than strontium and calcium carbonates. To partially substantiate this hypothesis, the experiments of ODUM (1951 A) are cited. He demonstrated that strontium existed as celestite and not strontianite as previously assumed in radiolaria. It is the intention of the authors to investigate this problem further and to determine the actual chemical composition of the strontium compound in such marine organisms as Madreporaria.

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Table I.—Chemical composition of calcareous portions of carbonate-secreting marine organisms

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
(A) MARINE ALGAE						
DIVISION RHODOPHYTA						
FAMILY CORALLINACEAE						
Bossea orbigniana	Calif.*	29·2	0·199	36·5	14·6	3·12
Bossea sp.	Calif.	27·0	0·201	34·7	18·0	3·41
Calliarthron cheilosporioides	Calif.	23·6	0·151	30·8	29·8	2·93
Corallina chilensis	Calif.	26·8	0·180	34·7	19·1	3·06
C. gracilis	Calif.	26·2	0·195	34·2	19·5	3·39
C. officinalis	N. H.	29·2	0·196	35·1	14·0	3·07
Corallina sp.	N. H.	26·6	0·186	33·1	19·1	3·19
Lithophyllum sp.	Calif.	29·2	0·203	34·5	16·3	3·18
Lithothamnion conchatum	Calif.	29·0	0·219	34·2	16·4	3·45
DIVISION CHRYSOPHYTA						
Coscinodiscus sp.	Wash.	trace	trace	4·1	18·9	—
(B) PHYLUM PROTOZOA, CLASS SARCODINA, ORDER FORAMINIFERA						
Calcarina sp.	Ifalik Atoll†	31·6	0·193	40·8	6·72	2·78
Baculogypsina sp.	Ifalik Atoll	31·4	0·217	40·8	9·40	3·16
Foraminifera (unidentified)	Bermuda	33·3	0·239	40·1	5·19	3·28

* The California specimens of algae were identified by Dr. G. J. HOLLENBERG.

† The Foraminifera specimens were collected by Professor DONALD ABBOTT and were identified y Mr. FRANK SULLIVAN.

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
(C) PHYLUM PORIFERA						
CLASS CALCAREA						
ORDER HOMOCOELA						
Leucosolenia eleanor	Calif.	1·29	trace	3·24	20·2	—
Leucosolenia sp.	Maine	13·6	0·099	23·3	25·0	3·33
Sponge (unidentified)	Beaufort Sea	13·5	0·098	34·4	22·8	3·34
ORDER HETEROCOELA						
Leuconia heathi	Calif.	1·00	trace	2·28	30·3	—
Rhabdodermella nuttingi	Calif.	29·6	0·149	35·8	12·7	2·30
CLASS DEMOSPONGIAE						
SUBCLASS TETRAXONIDA, ORDER EPIPOLASIDA						
Tethya aurantia	Calif.	0·06	trace	6·30	42·3	—
SUBCLASS CORNACUSPONGIDA						
ORDER POECILOSCLERINA						
Esperiopsis originalis	Calif.	0·08	trace	2·12	38·2	—
Ophlitaspogia pennata	Calif.	0·05	trace	1·97	40·8	—
ORDER HAPLOSCLERINA						
Haliclona permollis	Calif.	0·07	trace	6·57	42·2	—
ORDER KERATOSA						
Euspongia sp.	Unknown	0·05	trace	12·6	85·0	—
(D) PHYLUM COELENTERATA*						
CLASS HYDROZOA, ORDER MILLEPORINA						
Millepora tenera	Ifalik Atoll	38·1	0·686	41·4	3·15	8·22
ORDER STYLASTERINA						
Allopora californica	Calif.	36·5	0·778	38·5	8·46	9·74
A. campyleca paragea	Gulf of Alaska	35·7	0·768	40·6	4·47	9·83
A. porphyra	Calif.	38·8	0·580	41·1	2·91	6·83
A. venusta	Calif.	37·0	0·808	40·4	5·38	9·97
Cryptohelia trophostega	Bering Sea	37·8	0·930	41·1	3·42	11·2
Distichopora violacea	Marshall Is.	37·6	0·640	41·2	3·54	7·77
Errinopora zarhyncha	Aleutian Is.	37·5	0·224	43·1	2·50	2·73
Stylaster elegans	Marshall Is.	37·4	0·852	41·3	3·84	10·4
S. sanguineus	Hawaii	37·7	0·843	41·2	3·88	10·2
CLASS ANTHOZOA, SUBCLASS ALCYONARIA						
ORDER STOLONIFERA						
Tubipora sp.	Unknown	31·1	0·225	41·8	2·38	3·30
ORDER ALCYNACEA						
Eunephthya rubiformis	Beaufort Sea	4·72	0·039	12·4	30·4	3·78
ORDER PENNATULACEA						
Stylatula elongata	Calif.	22·7	0·128	28·5	33·0	2·64
ORDER GORGONACEA						
Psammogorgia arbuscula	Calif.	21·4	0·136	30·0	37·5	2·90
ORDER COENOTHECALIA						
Heliopora coerulea	Ifalik Atoll	37·3	0·618	40·0	6·60	7·57

* Some of the specimens were contributed by the Hopkins Marine Station from the collection of the late Professor W. K. FISHER.

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
SUBCLASS ZOANTHARIA, ORDER MADREPORARIA						
Acropora sp.	Ifalik Atoll	37·3	0·810	41·1	3·85	9·92
Astrangia sp.	Calif.	37·0	0·868	41·3	3·43	10·7
Balanophyllia elegans	Calif.	32·3	0·666	37·5	8·84	9·41
Caryophyllia sp.	Calif.	37·4	0·850	41·4	2·90	10·4
Meandrina sinuosa	Bermuda	36·5	0·802	41·2	3·25	10·1
Pocillopora sp.	Ifalik Atoll	37·9	0·735	41·5	3·13	8·85
Porites sp.	Ifalik Atoll	37·3	0·790	40·7	5·38	9·67
(E) PHYLUM ANNELIDA, CLASS POLYCHAETA						
FAMILY CIRRATULIDAE						
Dodecaceria pacifica	B.C., Canada*	32·5	0·574	40·6	5·38	8·07
D. fistulicola	Calif.	35·4	0·530	40·3	5·20	6·84
FAMILY SERPULIDAE						
Salmacina tribranchiata	Calif.	33·2	0·596	36·5	6·35	8·24
Serpula vermicularis	B.C., Canada	32·4	0·288	40·7	4·51	4·06
S. vermicularis	Calif.	32·1	0·289	42·5	4·60	4·12
Spirorbis sp.	N. H.	29·2	0·247	34·2	15·0	3·86
(F) PHYLUM ARTHROPODA, SUBPHYLUM MANDIBULATA, SUPERCLASS CRUSTACEA						
CLASS CIRRIPEDIA, ORDER THORACICA						
Balanus amphitrite	Florida†	37·0	0·428	41·8	5·00	5·28
B. balanoides	N. H.	37·6	0·382	41·7	3·27	4·64
B. balanoides	N. H.	34·1	0·336	39·8	7·76	4·50
B. cariosus	Wash.	39·1	0·324	42·2	1·80	3·78
B. crenatus	Beaufort Sea	36·1	0·337	41·7	3·24	4·27
B. eburneus	Florida	36·7	0·381	41·8	4·80	4·74
B. eburneus	Florida	36·6	0·345	41·7	2·39	4·32
B. glandula	Wash.	37·0	0·358	41·6	3·12	4·42
B. glandula	Calif.	37·4	0·371	41·5	2·88	4·53
B. nubilis	Calif.	35·6	0·334	39·6	7·18	4·29
B. nubilis	Wash.	34·2	0·282	36·7	12·3	3·77
Balanus sp.	Wash.	37·4	0·364	41·8	2·72	4·45
Balanus sp.	B.C., Canada	36·1	0·337	41·2	3·80	4·27
B. tintinnabulum	Calif.	37·2	0·381	41·4	1·88	4·67
Chthamalus fragilis	N. C.	32·4	0·328	37·3	8·33	4·62
Mitella polymerus	Calif.	36·8	0·344	40·7	4·48	4·27
Tetraclita squamosa	Calif.	35·6	0·381	41·2	4·07	4·88
CLASS MALACOSTRACA, SUBCLASS EUCARIDA, ORDER DECAPODA						
Cancer antennarius	Calif.	27·2	0·363	30·2	32·7	6·12
C. antennarius‡	Calif.	28·0	0·371	32·5	20·0	6·05
C. borealis	N. H.	24·0	0·322	29·3	27·2	6·13
C. magister	Wash.	24·0	0·351	28·1	28·1	6·69
C. productus	Calif.	23·3	0·308	30·2	30·0	6·04
*C. productus***	Calif.	0·44	trace	8·6	85·5	—
Hemigrapsus nudus	Wash.	26·0	0·349	29·3	28·7	6·13
Pugettia producta	Calif.	21·2	0·278	25·7	33·3	6·00
(G) PHYLUM MOLLUSCA						
CLASS AMPHINEURA, ORDER POLYPLACOPHORA						
Cryptochiton stelleri	Calif.	38·2	0·736	40·3	6·10	8·80
C. stelleri	Wash.	37·1	0·751	41·4	3·66	9·25
Cyanoplax hartwegii	Calif.	38·3	0·716	41·3	5·70	8·55
Nuttallina californica	Calif.	38·2	0·662	41·2	4·69	7·91
Tonicella lineata	Calif.	37·6	0·640	41·4	4·83	7·79

* The specimens from British Columbia were provided by Mr. CYRIL BERKELEY of the Pacific Biological Station.

† The Florida specimens were provided by Mr. C. S. YENTSCH.

‡ Claw ** Moulting

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
(G) PHYLUM MOLLUSCA (*continued*) CLASS AMPHINEURA, ORDER POLYPLACOPHORA						
Ischnochiton heathiana	Calif.	38·7	0·636	41·4	3·63	7·52
I. mertensii	Calif.	38·6	0·636	41·3	3·95	7·55
Ischnochiton sp.	Wash.	38·8	0·680	41·8	3·06	8·02
Katharina tunicata	Calif.	38·7	0·687	39·6	3·91	8·12
Mopalia ciliata	Calif.	37·2	0·626	41·1	4·83	7·69
M. lignosa	Calif.	37·9	0·664	41·2	4·26	8·01
M.muscosa	Calif.	37·9	0·608	41·0	4·74	7·32
M. muscosa	Wash.	37·8	0·709	42·2	3·31	8·57
M. wosnessenskii	Calif.	37·6	0·606	41·4	3·88	7·37
Chiton (unidentified)	Beaufort Sea	37·0	0·680	41·5	4·00	8·41
(H) PHYLUM MOLLUSCA, CLASS PELECYPODA ORDER FILIBRANCHIA FAMILY ANOMIIDAE						
Pododesmus macroschisma	Calif.	38·6	0·103	42·6	1·75	1·22
FAMILY MYTILIDAE						
Botula falcata	Calif.	38·6	0·196	38·9	5·67	2·32
Modiolus capax	Calif.	37·5	0·103	41·1	5·10	1·25
M. modiolus	N. H.	37·8	0·125	41·8	3·97	1·52
M. modiolus	N. H.	38·8	0·116	42·7	2·39	1·37
M. modiolus	N. H.	37·5	0·112	41·3	5·58	1·37
M. modiolus	N. H.	37·8	0·132	41·1	4·20	1·60
Modiolus sp.	Wash.	38·2	0·099	42·1	3·96	1·19
Mytilus edulis	N. H.	37·2	0·176	42·5	3·10	2·16
M. edulis	N. H.	37·9	0·110	42·0	3·32	1·33
M. edulis	Maine	38·3	0·128	42·1	3·30	1·53
M. edulis	Maine	37·2	0·116	42·4	3·52	1·43
M. edulis	Wash.	38·6	0·106	42·2	3·24	1·26
M. edulis	B.C., Canada	38·6	0·154	41·4	4·42	1·82
M. edulis	Beaufort Sea	36·6	0·117	41·2	5·53	1·46
M. edulis	Calif.	36·5	0·118	42·2	3·87	1·48
M. californianus	Calif.	39·0	0·086	43·1	1·54	1·01
M. californianus	Calif.	38·5	0·086	43·1	1·70	1·02
FAMILY PECTINIDAE						
Pecten hindsii	Wash.	38·2	0·111	41·8	1·91	1·33
P. hericius	Wash.	37·8	0·107	42·1	1·75	1·29
ORDER EULAMELLIBRANCHIA FAMILY OSTREIDAE						
Crassostrea virginica	N. H.	33·7	0·092	42·4	2·16	1·25
C. virginica	N. C.	37·8	0·107	41·8	2·34	1·29
Ostrea gigas	B.C., Canada	34·6	0·097	37·6	13·3	1·28
O. gigas	B.C., Canada	36·2	0·100	42·5	1·71	1·26
O. lurida	Calif.	38·6	0·085	42·5	1·68	1·01
FAMILY SPONDYLIDAE						
Spondylus sp.	unknown	38·0	0·128	41·6	1·67	1·54
FAMILY CHAMIDAE						
Chama pellucida	Calif.	36·8	0·142	42·3	2·47	1·76
FAMILY TELLINIDAE						
Macoma irus	Calif.	38·7	0·153	40·8	2·42	1·81
M. nasuta	Calif.	38·0	0·215	38·9	2·27	2·59
M. secta	Calif.	38·9	0·248	42·5	2·17	2·91
Tellina sp.	B.C., Canada	37·1	0·173	42·1	2·50	2·14

Table I (*cont.*)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
FAMILY SOLENIDAE						
Ensis directus	N. H.	37·0	0·164	41·9	3·47	2·03
Siliqua costata	N. H.	38·4	0·182	42·4	2·46	2·17
S. patula	Wash.	38·4	0·207	42·0	2·88	2·46
Solen sicarius	Calif.	38·1	0·116	42·9	1·66	1·39
FAMILY MACTRIDAE						
Mesodesma deauratum	N. H.	37·6	0·164	42·0	3·31	2·00
Schizothaerus nuttallii	Wash.	37·8	0·195	41·6	4·00	2·36
S. nuttallii	Calif.	39·1	0·177	42·6	1·79	2·07
Spisula solidissima	N. H.	38·2	0·216	42·0	2·58	2·58
FAMILY PLEUROPHORIDAE						
Cyprina islandica	N. H.	39·2	0·135	42·7	1·93	1·57
FAMILY CLINOCARDIIDAE						
Clinocardium nuttallii	Wash.	37·6	0·245	41·9	2·98	2·98
C. nuttallii	Wash.	38·5	0·188	41·8	3·68	2·23
C. nuttallii	Calif.	38·0	0·185	41·8	3·55	2·22
FAMILY VENERIDAE						
Compsomyax subdiaphana	Wash.	38·6	0·180	42·2	3·07	2·13
Irus lamellifer	Calif.	37·6	0·134	41·6	3·20	1·63
Protothaca staminea	Wash.	39·4	0·179	41·8	3·30	2·08
P. staminea	Calif.	38·2	0·149	42·0	2·45	1·78
P. tenerrima	Wash.	37·3	0·175	42·0	2·94	2·14
Saxidomus giganteus	Wash.	38·6	0·192	42·3	2·23	2·27
S. muttallii	Calif.	37·8	0·125	42·2	2·63	1·52
Tivela stultorum	Calif.	38·8	0·120	42·0	3·34	1·41
Venus mercenaria	Canadian Atlantic	38·6	0·148	42·5	2·38	1·75
FAMILY PERIPLOMATIDAE						
Periploma sp.	B.C., Canada	37·9	0·183	42·0	2·60	2·20
FAMILY LYONSIIDAE						
Mytilimeria nuttallii	Calif.	36·6	0·188	39·8	7·63	2·35
FAMILY MYIDAE						
Mya arenaria	Maine	38·6	0·246	42·2	2·44	2·91
M. arenaria	Wash.	38·7	0·238	42·3	2·28	2·81
M. arenaria	Oregon	38·8	0·181	42·3	2·48	2·12
M. arenaria	Wash.	38·3	0·181	42·2	2·22	2·16
FAMILY SAXICAVIDAE						
Panope generosa	Wash.	38·2	0·207	42·3	2·03	2·48
Saxicava sp.	Beaufort Sea	37·9	0·196	40·5	4·98	2·36
FAMILY PHOLADIDAE						
Pholadidea penita	Calif.	37·0	0·147	41·2	3·63	1·82
P. ovoidea	Calif.	38·7	0·192	42·2	2·36	2·27
Zirfaea crispata	N. H.	38·3	0·148	41·2	3·63	1·77
Z. pilsbryi	Calif.	39·0	0·230	42·5	2·30	2·70
(I) PHYLUM MOLLUSCA, CLASS GASTROPODA						
SUBCLASS PROSOBRANCHIA						
ORDER ASPIDOBRANCHIA, SUBORDER ZYGOBRANCHIA						
FAMILY FISSURELLIDAE						
Diodora aspera	Calif.	38·5	0·114	41·5	3·54	1·35
Fissurella volcano	Calif.	39·5	0·108	42·6	1·86	1·25
Megathura crenulata	Calif.	38·0	0·104	42·8	2·03	1·25
Megatebennus bimaculatus	Calif.	39·0	0·117	42·1	2·74	1·38

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
FAMILY HALIOTIDAE						
Haliotis cracherodii	Calif.	37·1	0·123	42·2	3·87	1·52
H. rufescens	Calif.	38·8	0·130	41·7	3·82	1·54
SUBORDER PATELLACEA FAMILY ACMAEIDAE						
Acmaea digitalis	Calif.	38·5	0·199	42·6	2·51	2·37
A. digitalis	Calif.	37·6	0·204	42·1	2·79	2·48
A. insessa	Calif.	37·8	0·183	42·4	2·84	2·21
A. limatula	Calif.	38·2	0·168	42·0	3·03	2·01
A. mitra	Calif.	37·2	0·161	42·4	2·61	1·98
A. mitra	Wash.	38·2	0·162	42·3	2·48	1·94
A. pelta	Calif.	37·6	0·151	40·4	3·39	1·84
A. persona	Calif.	37·6	0·201	42·0	3·16	2·45
A. scabra	Calif.	37·3	0·180	42·5	1·97	2·21
A. t. scutum	N. H.	38·4	0·180	41·8	3·28	2·14
A. t. scutum	Calif.	37·6	0·164	41·7	3·65	2·00
Lottia gigantea	Calif.	37·4	0·170	42·2	2·71	2·08
SUBORDER TROCHACEA FAMILY TROCHIDAE						
Calliostoma canaliculatum	Calif.	37·2	0·129	41·0	4·95	1·59
C. costatum	Calif.	37·0	0·122	41·2	2·96	1·51
C. gloriosum	Wash.	36·3	0·131	41·7	4·73	1·65
Tegula brunnea	Calif.	37·5	0·124	40·6	4·06	1·51
T. funebralis	Calif.	37·4	0·113	41·9	3·64	1·38
T. montereyi	Calif.	38·2	0·121	41·5	3·99	1·45
FAMILY TURBINIDAE						
Astraea inaequalis	Calif.	36·7	0·120	41·0	5·37	1·50
ORDER PECTINIBRANCHIA SUBORDER TAENIOGLOSSA FAMILY EPITONIIDAE						
Epitonium groenlandicum	Atlantic	37·0	0·118	41·9	3·07	1·46
Epitonium sp.	Calif.	36·8	0·120	41·2	4·80	1·49
FAMILY VERMETIDAE						
Petaloconchus montereyensis	Calif.	35·6	0·144	40·2	7·10	1·85
FAMILY LITTORINIDAE						
Littorina litorea	Maine	38·4	0·107	42·5	2·27	1·27
L. litorea	N. H.	38·7	0·107	42·8	1·84	1·26
L. palliata (= *L. obtusata*)	N. H.	37·2	0·142	41·0	2·72	1·74
L. planaxis	Calif.	37·8	0·155	42·4	2·62	1·87
L. rudis (= *L. saxatilis*)	N. H.	38·6	0·140	41·8	1·50	1·66
L. rudis	N. H.	37·5	0·125	41·7	4·39	1·53
L. scutulata	Calif.	38·4	0·121	42·5	2·77	1·44
FAMILY CALYPTRAEIDAE						
Crepidula adunca	Calif.	37·7	0·140	42·0	3·22	1·70
C. fornicata	Mass.	38·0	0·149	42·3	2·37	1·79
C. nummaria	Calif.	38·5	0·153	42·3	2·36	1·82
FAMILY NATICIDAE						
Polinices Heros	Mass.	37·7	0·121	42·2	2·96	1·47
P. draconis	Wash.	38·8	0·137	42·5	2·28	1·61
Natica sp.	Beaufort Sea	37·8	0·108	41·8	3·54	1·31
SUBORDER STENOGLOSSA FAMILY OLIVIDAE						
Oliva litterata	Florida	39·6	0·145	42·8	1·61	1·67
Olivella biplicata	Calif.	38·9	0·113	42·4	1·84	1·33

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
FAMILY FUSINIDAE						
Fusinus monksae	Calif.	35·5	0·115	40·1	4·27	1·48
FAMILY NASSARIIDAE						
Nassa obsoleta	N. H.	36·4	0·151	40·9	6·46	1·89
FAMILY MURICIDAE						
Acanthina spirata	Calif.	38·6	0·131	42·3	2·66	1·55
Murex pume	Florida	39·9	0·172	41·7	2·30	1·97
M. triolatus	Calif.	38·0	0·131	42·6	1·68	1·58
Thais canaliculata	Calif.	38·1	0·128	42·8	2·26	1·54
T. emarginata	Calif.	37·6	0·138	42·3	3·03	1·68
T. lamellosa	Wash.	38·8	0·129	42·8	1·45	1·52
T. lapillus	N. H.	38·5	0·126	42·7	1·13	1·50
T. lapillus	N. H.	36·5	0·128	39·4	3·68	1·60
SUBCLASS OPISTHOBRANCHIA, ORDER NUDIBRANCHIA						
Anisodoris nobilis	Calif.	2·60	0·063	3·25	67·2	11
Archidoris montereyensis	Calif.	3·16	0·062	4·68	78·0	9
Triopha grandis	Calif.	0·25	trace	(——91·3——)		—
(J) PHYLUM MOLLUSCA CLASS SCAPHOPODA						
Dentalium entale	Wash.	38·2	0·196	42·3	1·81	2·35
CLASS CEPHALOPODA, SUBCLASS DIBRANCHIATA, ORDER DECAPODA						
Loligo opalescens	Calif.	trace	trace	trace	99·5	—
Sepia sp.	unknown	35·8	0·293	40·1	7·35	3·74
(K) PHYLUM BRYOZOA, CLASS ECTOPROCTA ORDER CYCLOSTOMATA						
Idmonea sp.	Calif.	35·6	0·307	38·1	7·90	3·94
Crisia sp.	Calif.	35·7	0·282	38·2	6·28	3·61
Bryozoa (unidentified)	Beaufort Sea	34·3	0·256	40·2	7·30	3·41
Bryozoa (unidentified)	Beaufort Sea	30·6	0·209	35·0	16·5	3·12
Bryozoa (unidentified)	Beaufort Sea	25·3	0·181	31·8	23·2	3·27
ORDER CHEILOSTOMATA						
Bugula californica	Calif.	18·2	0·124	23·7	36·0	3·12
Hippodiplosia insculpta	Calif.	29·4	0·247	35·8	13·8	3·84
Phidolopora pacifica	Calif.	33·7	0·221	40·0	6·37	3·00
(L) PHYLUM BRACHIOPODA, CLASS ARTICULATA, ORDER TESTICARDINES						
Hemithyris psittacea	Beaufort Sea	37·7	0·113	42·2	3·02	1·37
*H. psittacea**	Beaufort Sea	38·9	0·102	42·8	1·94	1·20
Terebratalia transversa	Wash.	38·0	0·130	41·3	2·02	1·57
Terebratulina unguicula	Calif.	37·8	0·113	42·5	1·81	1·37
Brachiopoda (unidentified)	Calif.	38·7	0·108	42·7	1·79	1·28
(M) PHYLUM ECHINODERMATA CLASS CRINOIDEA						
Antedon sp.	Calif.	25·8	0·145	38·2	13·3	2·56
CLASS ASTEROIDEA ORDER FORCIPULATA						
Asterias forbesi	Mass.	18·6	0·113	24·9	39·4	2·78
A. vulgaris	N. H.	22·5	0·141	27·9	33·6	2·86
A. vulgaris	Mass.	20·2	0·128	28·6	34·4	2·89
Leptasterias aequalis	Calif.	20·9	0·127	32·7	31·0	2·78
L. pusilla	Calif.	25·5	0·146	37·7	20·4	2·61
Mediaster aequalis	Calif.	27·3	0·158	36·1	19·0	2·60

* Remains.

Table I (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \times 1000$
CLASS ASTEROIDEA (*continued*)						
ORDER FORCIPULATA						
Pisaster brevispinus	Calif.	22·7	0·131	33·6	28·5	2·64
P. giganteus	Calif.	17·2	0·101	31·9	37·2	2·69
P. ochraceus	Calif.	24·6	0·148	34·0	24·4	2·76
Pycnopodia helianthoides	Calif.	20·0	0·114	31·8	33·5	2·60
ORDER SPINULOSA						
Henricia leviuscula	Wash.	23·1	0·136	30·3	28·6	2·69
H. leviuscula	Calif.	25·2	0·155	33·3	25·8	2·81
H. sanguinolenta	N. H.	18·4	0·112	28·6	38·2	2·78
Henricia sp.	Beaufort Sea	20·6	0·125	29·0	34·0	2·78
Solaster papposus	Beaufort Sea	23·2	0·131	31·0	28·8	2·60
Patiria miniata	Calif.	26·8	0·162	36·1	21·2	2·77
ORDER PHANEROZONIA						
Hippasteria spinosa	Wash.	22·7	0·137	30·8	29·6	2·76
Luidia sp.	Calif.	24·1	0·142	34·1	19·3	2·69
CLASS OPHIUROIDEA						
ORDER EURYALAE						
Gorgonocephalus sp.	Beaufort Sea	26·6	0·158	33·4	21·8	2·72
ORDER OPHIURAE						
Amphipholis squamata	Calif.	24·7	0·146	33·2	23·5	2·70
Ophiopholis aculeata	Maine	24·5	0·146	32·6	24·4	2·72
O. aculeata	N. H.	25·9	0·149	34·5	19·7	2·63
Ophiothrix spiculata	Calif.	20·4	0·118	28·9	33·4	2·64
Ophioplocus esmarki	Calif.	27·1	0·165	36·9	17·0	2·79
Ophiura sarsii	Wash.	31·2	0·185	39·2	11·0	2·71
O. sarsii	Beaufort Sea	30·2	0·175	38·0	13·5	2·65
CLASS ECHINOIDEA						
ORDER CENTRECHINOIDA						
Strongylocentrotus dröbachiensis	N. H.	34·8	0·214	41·0	5·68	2·81
S. dröbachiensis	Wash.	35·5	0·214	42·0	3·33	2·76
S. dröbachiensis	Wash.	35·6	0·210	42·0	3·05	2·70
S. fragilis	Calif.	32·7	0·188	39·6	9·28	2·63
S. franciscanus	Wash.	36·4	0·218	42·8	2·97	2·74
S. pallidus	Beaufort Sea	32·2	0·191	40·0	8·10	2·71
S. purpuratus	Wash.	35·4	0·215	43·8	2·18	2·78
S. purpuratus	Calif.	33·2	0·210	41·4	6·96	2·89
Heterocentrotus trigonarius	Ifalik Atoll	31·6	0·180	43·9	1·20	2·60
ORDER CLYPEASTROIDA						
Dendraster excentricus	Calif.	33·5	0·205	43·5	2·85	2·79
Echinarachnius parma	N. H.	31·8	0·178	41·4	5·62	2·56
ORDER SPATANGOIDEA						
Brisaster sp.	Wash.	30·5	0·164	40·1	8·77	2·46
CLASS HOLOTHUROIDEA						
ORDER DENDROCHIROTIDA						
Cucumaria curata	Calif.	0·8	trace	7·5	84·0	—
Psolus chitonoides	Wash.	29·1	0·173	38·3	12·2	2·72
P. peroni	Beaufort Sea	25·2	0·153	32·1	25·8	2·78
P. sp.	Calif	28·6	0·170	34·5	18·0	2·72
(N) PHYLUM CHORDATA, CLASS ASCIDIACEA						
Polyclinum planum	Calif.	0·30	trace	13·8	70·0	—
Synoicum par-fustis	Calif.	0·38	trace	13·5	69·1	—

Table II.—The occurrence of calcium and strontium in substances other than marine organisms

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
Walrus (*Odobenus rosmarus*) ivory	Alaska	21·0	trace	2·96	36·8	—
Fresh water clam (unidentified)	Wash.	38·0	0·085	41·4	5·53	1·02
Fresh water clam (unidentified)	Wash.	36·4	0·072	41·3	6·02	0·90
Potamobius sp.	Wash.	19·8	0·077	21·7	45·5	1·78
Deep sea sediments*	Indian Ocean (Swedish Deep Sea Expedition 1948–1949)	29·4	0·125	37·7	2·95	1·94
Globigerina ooze†	Pacific Ocean	37·5	0·122	41·8	1·46	1·49
Coquina rock (cemented shells)	Florida	37·8	0·153	41·7	1·57	1·85
Limestone deposits	Wash.	38·1	0·052	42·5	0·68	0·63
Strontianite deposits	Wash.	3·56	52·5	31·5	0·26	6,750
Sea water	Over-all					8·90

* Specimen was provided by Mr. Taivo Laevastu.

† Specimen was provided by Dr. Howard R. Gould.

Table III.—Summary of results arranged in accordance with the phylogenetic classification of marine organisms

Classification	Calcium mean %	Strontium mean %	Carbon dioxide mean %	Organic matter mean %	Mean atom ratio $\frac{Sr}{Ca} \times 1000$
Marine Algae, Corallinaceae	27·4	0·193	34·2	18·5	3·20
Protozoa, Foraminifera	32·1	0·216	40·6	7·10	3·07
Porifera, Calcarea	11·8	0·069	19·8	22·2	2·99
Demosponiae	0·06	trace	5·91	49·7	—
Coelenterata, Hydrozoa	37·4	0·711	41·0	4·16	8·69
Anthozoa					
Alcyonaria	23·2	0·229	30·5	22·0	4·04
Zoantharia	36·5	0·789	40·7	4·40	9·86
Annelida, Polychaeta	32·5	0·421	39·1	6·84	5·87
Arthropoda, Cirripedia	36·3	0·354	40·8	4·65	4·45
Decapoda	24·6	0·328	29·3	27·8	6·17
Mollusca, Amphineura	38·0	0·669	41·2	4·30	8·06
Pelecypoda	37·9	0·154	41·8	3·18	1·85
Gastropoda					
Prosobranchia	37·8	0·139	41·8	3·14	1·68
Opisthobranchia	2·38	0·062	3·97	72·6	10
Scaphopoda	38·2	0·196	42·3	1·81	2·35
Cephalopoda	35·8	0·293	40·1	7·35	3·74
Bryozoa, Ectoprocta	30·4	0·228	35·4	14·7	3·41
Brachiopoda, Articulata	38·4	0·113	42·3	2·12	1·36
Echinodermata, Crinoidea	25·8	0·145	38·2	13·3	2·56
Asteroidea	22·4	0·134	31·8	29·3	2·73
Ophiuroidea	26·3	0·153	34·6	20·5	2·69
Echinoidea	33·6	0·199	41·8	5·00	2·70
Holothuroidea	27·8	0·166	35·0	18·3	2·74
Chordata, Ascidiacea	0·34	trace	13·7	69·6	—

Table IV.—Strontium-calcium atom ratio of marine invertebrates collectea at different tide levels

Mid-tidal Level	Atom ratio $\frac{Sr}{Ca} \times 1000$	Low Inter-tidal Level	Atom ratio $\frac{Sr}{Ca} \times 1000$
Mytilus californianus	1·01	*Diodora aspera*	1·35
Littorina scutalata	1·44	*Rhabdodermella nuttingi*	2·30
Pisaster ochraceus	2·76	*Henricia leviscula*	2·81
Mitella polymerus	4·27	*Tetraclita squamosa*	4·88
Balanus glandula	5·06	*Pugettia producta*	6·00
Cancer antennarius	6·12	*Cryptochiton stelleri*	8·80
Nuttallina californica	7·91	*Balanophyllia elegans*	9·41
		Anisodoris nobilis	11

Table V.—Strontium-calcium atom ratio of Echinodermata in relation to their habitats

Habitat	Specimen	Atom ratio $\frac{Sr}{Ca} \times 1000$
Wharf Piling	*Pisaster giganteus*	2·69
Mid-tidal Level Rocky Shore	*P. ochraceus*	2·76
Low Inter-tidal Rocky Reef	*Henricia leviscula*	2·81
Burrowing	*Strongylocentrotus purpuratus*	2·89
Sandy Flat	*Dendraster excentricus*	2·79
Sandy-mud Substratum	*Ophioplocus esmarki*	2·79
Inter-tidal Zone	*Psolus* sp.	2·72
Deep water	*Strongylocentrotus fragilis*	2·63

Table VI.—Strontium-calcium atom ratio in relation to the mineralogical character of calcium carbonate in marine organisms

Calcite	Atom ratio $\frac{Sr}{Ca} \times 1000$	Calcite–Aragonite Mixture	Atom ratio $\frac{Sr}{Ca} \times 1000$	Aragonite	Atom ratio $\frac{Sr}{Ca} \cdot 1000$
Algae, Corallinaceae	3·20	Mollusca,		Coelenterata,	
Protozoa,		Pelecypoda	1·94†	Hydrozoa	9·49‡
Foraminifera	3·07	Gastropoda		Zoantharia	9·86
Porifera, Calcarea	2·99	Prosobranchia	1·68	Mollusca,	
Coelenterata,				Amphineura	8·06
Alcyonaria	3·16*			Gastropoda	
Arthropoda,				Nudibranchia	10
Cirripedia	4·45			Scaphopoda	2·35
Mollusca,				Cephalopoda	3·74
Pelecypoda					
Anomiidae	1·22				
Ostreidae	1·22				
Pectinidae	1·31				
Bryozoa, Ectoprocta	3·41				
Brachiopoda,					
Articulata	1·36				
Echinodermata	2·71				

* Does not include the aragonite *Heliopora*.

† Does not include the calcite Anomiidae, Ostreidae and Pectinidae.

‡ Does not include the calcite *Errinopora*.

REFERENCES

Asari, Tamiya (1950), Geochemical distribution of strontium. VII. Strontium contents of shells. *J. Chem. Soc., Japan*, **71,** 156–158.

Bøggild, O. B. (1930), The shell structure of the molluscs. *Kl. Danske Videnskab. Selskab, Skrifter, Naturvidenskab. math. Afdel.*, (9) **2,** 231–326.

Chave, E. K. (1954), Aspects of the biogeochemistry of magnesium. I. Calcareous marine organisms. *J. Geol.*, **62,** 266–283.

Chow, T. J. and Thompson, T. G. (1955 a), Flame photometric determination of strontium in sea water. *Anal. Chem.*, **27,** 18–21.

Chow, T. J. and Thompson, T. G. (1955 b), Flame photometric determination of calcium in sea water and marine organisms. *Anal. Chem.* **27,** 910-913.

Clarke, F. W. and Wheeler, W. C. (1922), Inorganic constituents of marine invertebrates. *Prof. pap. U.S. Geol. Sur.*, No. 124, 1–62.

Dieulafait, L. (1877), La strontiane, sa diffusion dans la nature minérale. *C.R. Acad. Sci., Paris*, **84,** 1303–1305.

Forchhammer, G. (1852), Beiträge zur Bildungsgeschichte des Dolomits. *N. Jb. Min. Geol. Paläont.*, p. 854.

Fox, H. M. and Ramage, H. (1931), A spectrographic analysis of animal tissues. *Proc. Roy. Soc., London*, **B, 108,** 157–173.

Kulp, J. L., Truekain, Karl and Boyd, D. N. (1952), Strontium content of limestones and fossils, *Bull. Geol. Soc. Amer.*, **63,** 701–716.

Lowenstam, H. A. (1954 a), Environmental relations of modification compositions of certain carbonate secreting marine invertebrates. *Proc. Nat. Acad. Sci., U.S.A.*, **40,** 39–48.

Lowenstam, H. A. (1954 b), Factors affecting the aragonite-calcite ratios in carbonate secreting marine organisms. *J. Geol.*, **62,** 284–321.

McCance, R. A. and Masters, M. (1937), The chemical composition and the acid base balance of *Archidoris britannica. J. Mar. Biol. Ass., U.K.*, **22,** 273–279.

Moretti, Giuseppe (1813), Sur le sulfate de strontiane trouvé dans le corps marins pétrifés, et sur deverses combinaisons de cette terre avec quelques acides. *Ann. Chem., Paris*, (1) **86,** 262–273.

Noll, W. (1934), Geochemie des Strontiums. *Chem. Erde*, **8,** 507–600.

Odum, H. T. (1951 a), Note on the strontium content of sea water, celestite Radiolaria, and strontianite snail shells. *Science*, **114,** 211–213.

Odum, H. T. (1951 b), The stability of the world strontium cycle. *Science*, **114,** 407–411.

Rankama, K. and Sahama, T. G. (1949). *Geochemistry*, p. 226, The University of Chicago Press, Chicago.

Schmelck, L. (1901), Chemical examination of shells of Mollusca and dried Echinodermata. *Norweg. N. Atl. Exper.*, 1876–1878, *Zoology*, **7**: (28), 129.

Trueman, E. R. (1944), Strontium in molluscan shells. *Nature*, **135,** 142.

Tsuchiya, Yasuhiko (1944), Distribution of strontium in calcareous organisms. I. Strontium content of reef-forming corals. *J. Agr. Chem. Soc., Japan*, **20,** 653–654.

Tsuchiya, Yasuhiko (1948), Studies on the method for the preparation of strontium from corals and calcareous algae. *J. Fac. Agric.*, Kyushu Univ., Japan, **9,** 65–68.

Vinogradov, A. P. (1953), *The Elementary Chemical Composition of Marine Organisms.* Sears Foundation for Marine Research, Memoir II. Yale University, New Haven.

Vinogradov, A. P. and Borovik-Romanova, T. F. (1945), Geochemistry of strontium. *C.R. Acad. Sci., U.S.S.R.*, **46,** 193–196.

Vogel, H. August von (1814), Researches analytiques sur le corail rouge. *Ann. Chim., Paris*, (1) **89,** 113–134.

Wattenberg, H. and Timmermann, E. (1936), Uber die sättigung des Seewasser an $CaCO_3$, und die anorganogene Bildung von Kalksedimenten. *Ann. d. Hydrogr. u. Mar. Meteor.*, pp. 23–31.

Wattenberg, H. and Timmermann, E. (1938), Die Löslichkeit von Magnesiumkarbonate und Strontiumkarbonate in Seewasser. *Kieler Meeresforchungen*, **2,** 81–94.

Webb, D. A. (1937), Studies on the ultimate composition of biological material. II. Spectrographic analysis of marine invertebrates with special reference to the chemical composition of their environment. *Sci. Proc. Roy. Dublin Soc.*, **21,** 505–539.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 40-44.

Variation, en mer, de la teneur en oxygène dissous au proche voisinage des sédiments

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Summary—The experiments reported in this paper show that the oxygen content of the water undergoes a rapid decrease in the immediate vicinity of the bottom. This decrease is related to the very rapid oxidation of the sediment and the very slow diffusion of the dissolved gas.

A LA SUITE d'une série de dosages exécutés au large de Monaco en 1952 (Brouardel et Fage, 1954), sur des échantillons d'eau prélevés à l'aide de carottiers de divers modèles, par des fonds de 200 à 1000 m, nous avions conclu que la teneur en O_2 dissous décroît brusquement au proche voisinage des sédiments et nous émettions alors l'hypothèse que cette diminution de la teneur en O_2 pourrait être plus importante encore au ras même du sédiment.

De nouvelles recherches poursuivies en 1953–54 à l'aide d'appareils construits en conséquence ont eu pour but de préciser ce point.

Trois appareils différents ont servi aux prélèvements destinés à ces recherches, tous trois ont le caractère commun d'être entièrement en matière plastique. Le tube préleveur est constitué par un cylindre de plexiglas complétement ouvert à ses extrémités; ainsi, d'une part, il ne peut se produire aucune oxydation, d'autre part, il n'y a pas de perte de charge et donc de mélange d'eau dû à des étranglements ou des soupapes.

Carottier. Simple tube en plexiglas (fig. 1) de 1 m de long sur 5 cm de diamètre. A l'extrémité supérieure un clapet en matière plastique est maintenu complétement éclipsé à la descente de l'appareil par un ergot auquel est fixé le câble du treuil. Lorsque le tube touche le fond, le câble en prenant du mou libère le clapet qui, sous l'action de deux ressorts en acier inoxydable, maintient hermétiquement fermée l'extrémité supérieure du tube. L'extrémité inférieure étant bouchée par la carotte, lorsque le tube rencontre le sédiment il se trouve simultanément fermé à ses deux extrémités et emprisonne une véritable carotte d'eau.

Le fonctionnement du carottier, facilement contrôlé au cours de plongées grâce à la parfaite transparence du plexiglas, montre que, convenablement lesté, il découpe le sédiment exactement " à l'emporte pièce ", sans mettre en suspension de particules de vase au-dessus de la carotte.

Bouteille de prélèvement. Cette bouteille (fig. 2) est destinée a faire des prélèvements non plus au ras du sédiment, mais à une hauteur déterminée au-dessus de celui-ci (5 m dans nos expériences). Le corps de l'appareil est ici encore formé d'un simple tube en plexiglas à chacune des extrémités duquel un clapet, en même matière, est maintenu à la descente totalement eclipsé par un ergot. Le système de déclenchement des clapets est basé sur un principe analogue à celui d'une arbalète dont la corde est constituée par le câble du treuil. Le carotier, fixé à l'extrémité du câble, maintient bandée cette arbalète par la tension qu'il exerce sur celui-ci. Dès que le carottier touche le fond, le câble détendu libère les ergots des clapets qui se ferment simultanément sous l'action de deux ressorts.

Préleveur de la surface du sédiment (fig. 3). Le principe de cet appareil est celui du "Jenkins surface mud sampler " qui est employé en Limnologie. Mais, ici encore, cet appareil est entièrement réalisé en matière plastique ce qui lui procure une remarquable souplesse de fonctionnement indispensable à la mer. La bouteille elle-même est un tube de plexiglas de 60 cm de long et de 7 cm de diamètre supportée par un bâti. Deux clapets, sortes de paupières, eclipsés à la descente, sont libérés dès que

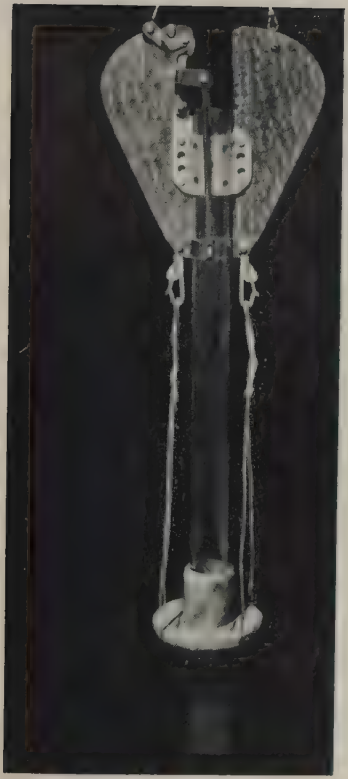

Fig. 1. Carottier à la descente, clapet ouvert.

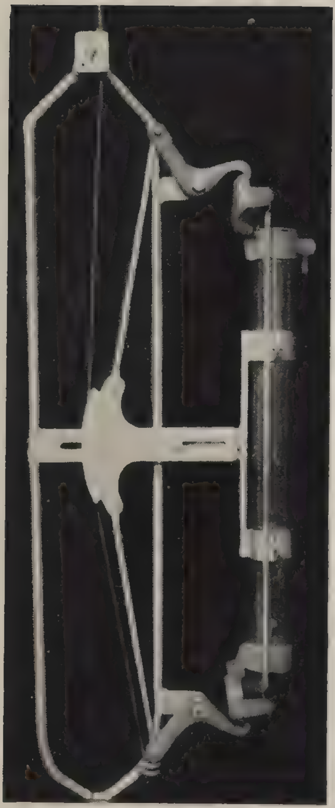

Fig. 2. Bouteille de prélèvement.

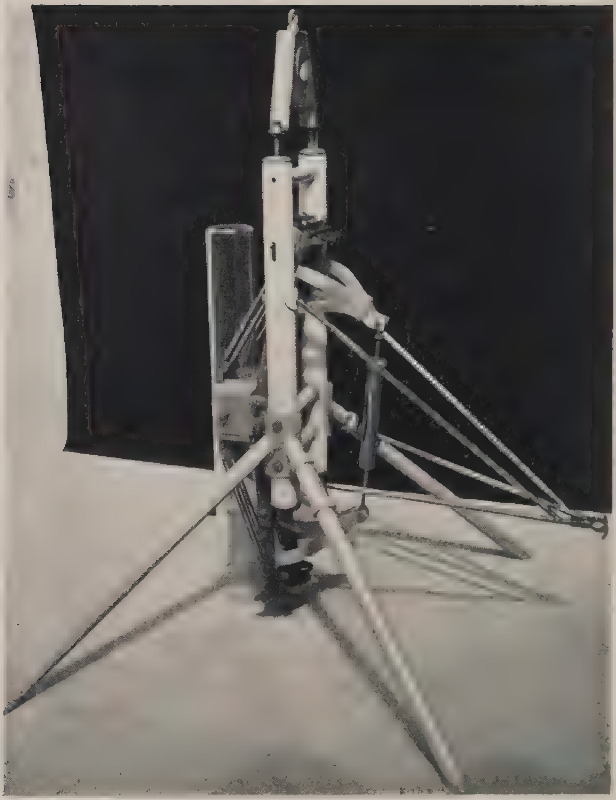

Fig. 3. Préleveur de surface, clapets ouverts

l'appareil touche le fond, puis soumis à l'action de deux jeux de quatre ressorts qui les entraînent avec puissance, mais aussi avec lenteur grâce à l'action d'un frein hydraulique. Le clapet situé à la partie inférieure découpe la pellicule superficielle du sédiment (2 à 3 cm d'épaisseur) ainsi retenue dans le tube. A le remontée les deux clapets ferment hermétiquement les extrémités de la bouteille.

Contrairement au carottier qui est descendu trés rapidement afin de faire une carotte suffisamment importante pour boucher l'extrémité inférieure du tube, cet appareil est descendu extrêmement lentement dès l'approche du fond et véritablement " posé " sur celui-ci.

L'exposé suivant à trait aux résultats obtenus avec ces appareils simultanément employés au cours des sorties effectuées en Juin-Juillet 1954 avec l'*Eider*, bateau du Musée Océanographique.

Distinguant parfaitement dans le carottier, grâce à la transparence du plexiglas, la limite de la carotte et de l'eau limpide emprisonnée au-dessus d'elle, il est possible de faire des prélèvements par siphonage, grâce à un fin tube de verre. Les niveaux choisis pour ces prélèvements ont été les suivants: au ras du sédiment, toutefois sans atteindre la carotte, puis à 5—10—25—40—55 cm de celui-ci.

En outre, comme lors des expériences antérieures (Brouardel et Fage, 1953), la bouteille-arbalète, suspendue au même câble, était disposée à 5 m au-dessus du carottier faisant donc un prélèvement d'eau à environ 6 m au-dessus du sédiment.

Les teneurs en O_2 de l'eau des divers échantillons obtenus dans ces conditions figurent au tableau I. Ces teneurs y sont exprimées en milligrammes par litre.

Tableau I

Teneur en O_2 de l'eau prélevée à l'aide des appareils (*Figs.* 1 *et* 2) *au-dessus du sédiment*

Profondeur:	100 *m*	140 *m*	210 *m*	220 *m*	240 *m*	245 *m*	290 *m*	305 *m*	*Moyennes*
5 m	7,89	7,33	7,07	6,95	6,94	6,37	6,41	6,34	6,92 mg/l
55 cm	7,88	7,23	6,84	7,20	6,86	6,81	6,27	6,21	6,91
40	7,76	7,23	6,93	6,80	6,58	6,79	6,50	6,48	6,88
25	7,83	7,23	7,13	6,78	6,60	6,40	6,42	6,36	6,84
10	7,71	7,56	7,11	6,76	6,39	6,46	6,47	6,22	6,83
5	7,83	7,13	6,67	6,58	6,75	6,47	6,37	6,42	6,78
au ras du sédiment	7,66	6,92	6,59	6,65	6,67	5,61	6,31	6,35	6,59

Sur la Figure 4, nous avons reporté en abscisses les teneurs moyennes en O_2 des prises aux différentes hauteurs (ordonnées) au-dessus du sédiment. Cette courbe fait apparaître, avec plus de netteté que celles obtenues lors des expériences antérieures, la diminution rapide de taux d'O_2 au proche voisinage du sédiment. L'amélioration due au remplacement de l'afcodur du carottier par le plexiglas transparent permet, en effet, de faire les prélèvements plus près de la carotte, à des hauteurs mieux déterminées, et d'avoir ainsi l'allure de la courbe dans les premiers centimètres.

On voit qu'entre la teneur en O_2 de l'échantillon d'eau prélevé par la bouteille à 5 m au-dessus du sédiment et celle de l'eau prélevée à la partie supérieure du carottier on n'observe pratiquement aucune différence. Par contre, la teneur en O_2 de l'eau renfermée dans le carottier diminue rapidement, et cela d'autant plus que l'on se rapproche de la carotte. Dans les expériences antérieures (carottier à clapet, puis carottier en afcodur) les différences entre les moyennes des taux d'O_2 observés entre les deux étages extrêmes étaient de 3,7 et 3,5 %. Ici, la différence moyenne entre les prélèvements extrêmes faits dans le carottier, à 55 cm l'un de l'autre, est de 0,32 mg soit 5 %.

Si le carottier employé ici présentait une amélioration sur les précédents il restait, dans son usage, un point sur lequel aucun calcul ne pouvait donner d'appréciation mais qui pouvait, pensions-nous, présenter de l'importance.

En effet, pour que la colonne d'eau reste emprisonnée dans le tube il fallait à son extrémité inférieure une carotte relativement importante. Pour cela une assez grande vitesse de descente était nécessaire et nous ne savions dans quelle mesure cette vitesse ne risquait pas de perturber la position des couches d'eau lors de la rencontre du carottier avec le sédiment. D'autre part, à la remontée la carotte risque toujours de glisser légèrement le long du tube et de modifier peut-être, la position de l'eau. C'est pour éliminer ces causes possibles de perturbation que nous nous sommes servis d'un appareil de principe différent, c'est-à-dire du préleveur de surface dont nous avons donné plus haut une sommaire description.

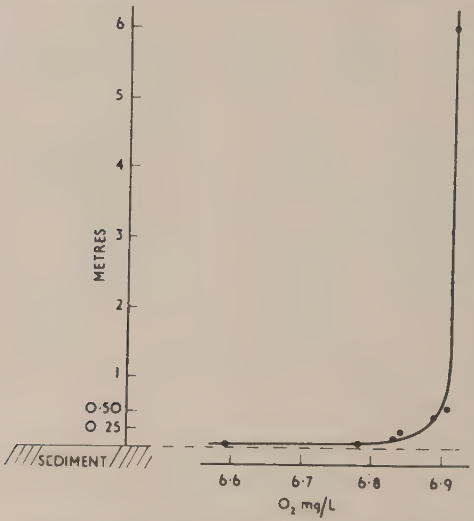

Fig. 4. Teneurs en O_2 de l'eau dans une couche de 6 m d'épaisseur au dessus du sédiment (Carottier et Bouteille de prélévement).

Cette bouteille " carottier d'eau " et le carottier en plexiglas ont été utilisés simultanément au cours des sorties de l'*Eider* en Juin-Juillet 1954, puis elle a été utilisée avec la bouteille-arbalète, par de plus grandes profondeurs, en Octobre 1954 à bord de la *Calypso*.

Les prélèvements, comme dans le cas du carottier, se faisaient par siphonage dont la technique était d'ailleurs améliorée ici par l'emploi d'une " pige " qui guidait le fin tube de verre dans le carottier bouteille.

Lors des sorties de Juin-Juillet, les prélèvements faits à des hauteurs de 1, 5, 10, 25 et 40 centimètres, au-dessus de la pellicule découpée par le clapet inférieur de la bouteille, ont donné les résultats qui figurent au tableau II et qui permettent de construire la courbe figure 5.

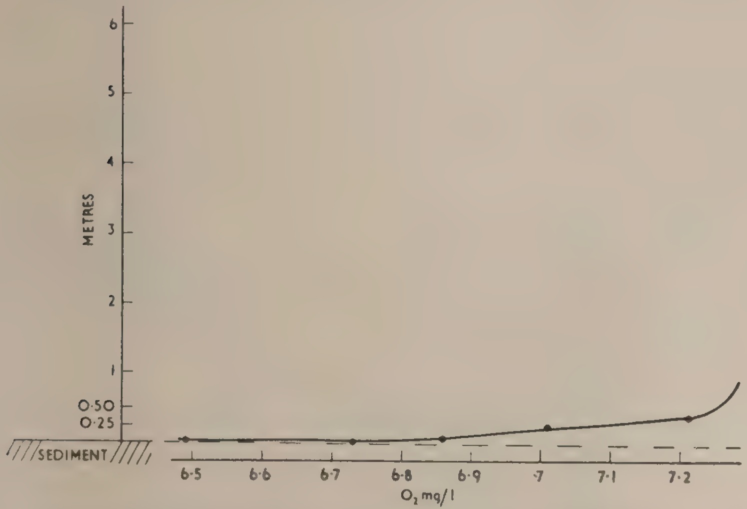

Fig. 5. Teneurs en O_2 de l'eau dans une couche de 40 cm d'épaisseur au-dessus du sédiment (Préleveur de surface).

Tableau II

Teneur en O_2 de l'eau prélévee à l'aide de l'appareil (*Fig.* 3), *au-dessus du sédiment*

Profondeur:	85 *m*	95 *m*	130 *m*	150 *m*	150 *m*	180 *m*	220 *m*	230 *m*	235 *m*	245 *m*	250 *m*	255 *m*	275 *m*	285 *m*	430 *m*	*Moyennes*
40 cm	7,89	7,95	7,53	7,83	7,44	7,36	7,08	7,44	7,07	6,90	6,65	7,08	6,73	7	6,17	7,21 mg/l
25 cm	7,89	7,89	7,53	7,64	7,34	7,24	6,94	6,93	7,09	6,74	6,27	6,96	6,63	6,77	6,91	7,05
10 cm	7,68	7,51	7,45	7,42	7,31	7,07	6,90	6,60	6,89	5,92	6,14	7,07	6,54	6,46	5,88	6,86
5 cm	7,57	7,59	7,25	7,38	6,68	6,54	6,79	6,16	6,64	6,68	6,24	6,82	6,39	6,37	5,82	6,73
au ras du sédiment	7,36	7,27	7,04	7,05	6,50	6,39	6,47	6,21	6,57	5,54	6,05	6,35	6,36	6,48	5,74	6,49

La courbe figure 6, déduite du tableau III a trait aux résultats obtenus en Octobre. Elle confirme, à une autre époque et pour d'autres profondeurs, l'allure de la courbe précédente.

Si l'on compare maintenant cette diminution du taux d'O_2 avec celle due normalement à l'augmentation de la profondeur, mais en opérant alors largement au-dessus du sédiment, on constate que celle-ci est seulement de l'ordre de 0,15 mg/l par 100 m ce qui représente sur 10 cm une variation de—0,00015 mg/l, et cela dans la région où nous opérions, à la même époque et à la même profondeur moyenne. Or dans les 10 cm d'eau au-dessus du sédiment cette variation est (tableau II) de—0,37 mg/l, soit

Tableau III

Teneur en O_2 de l'eau prélévee à l'aide des appareils (*Figs.* 2 *et* 3) *au-dessus du sédiment*

Profondeur:	110 *m*	160 *m*	870 *m*	950 *m*	1740 *m*	*Moyennes*
5 m	7,36	7,01	6,97	7,36	6,45	7,03 mg/l
40 cm	7,21	7,02	6,86	7,46	6,33	6,96
25 cm	7,18	6,98	6,85	7,04	6,24	6,86
10 cm	7,10	6,53	6,59	7,21	6,17	6,72
5	7,14	6,60	6,45	6,75	6,04	6,6
au ras du sédiment	7,06	6,30	5,87	6,69	5,83	6,35

4×10^4 fois plus. On peut donc véritablement parler d'une *chute* du taux d'oxygène au ras du sédiment.

Ces dernières expériences ont donc permis de préciser l'allure de la variation du taux d'O_2 au très proche voisinage du sédiment et ont montré qu'au fur et à mesure que les techniques de prélèvements s'améliorent cette variation apparaît encore plus nettement sur les courbes. Le sédiment constitue donc une couche puissamment réductrice, cause du phénomène que nous analysons.

Nous avons alors essayé de déterminér à quelle vitesse se fait cette oxydation. Avec les précautions nécessaires, nous avons étalé sur 5 cm d'épaisseur, au fond d'un bac, d'une contenance de 380 litres, 30 litres de sédiment prélevé au large et dont la couche supérieure avait été desséchée à l'étuve à 110° C. Le bac, haut de 55 cm, étant rempli d'eau de mer de teneur en O_2 connue, nous avons, chaque jour, dosé les variations de cette teneur à différents niveaux. Il a été constaté que, dans la couche d'eau de 1 cm d'épaisseur au contact du sédiment, la teneur en O_2 s'abaisse si rapidement qu'au bout de 30 heures elle a diminué de moitié; au bout de trois jours, elle n'est plus que de l'ordre du milligramme et, au bout de neuf jours, elle est si faible qu'elle ne peut plus être mise en évidence par des méthodes sensibles au 2/100e de milligramme: cette couche d'eau ne contient pratiquement plus d'oxygène. Pendant le même temps, la couche située seulement à 10 cm au-dessus n'a perdu que 0,5 mg l.

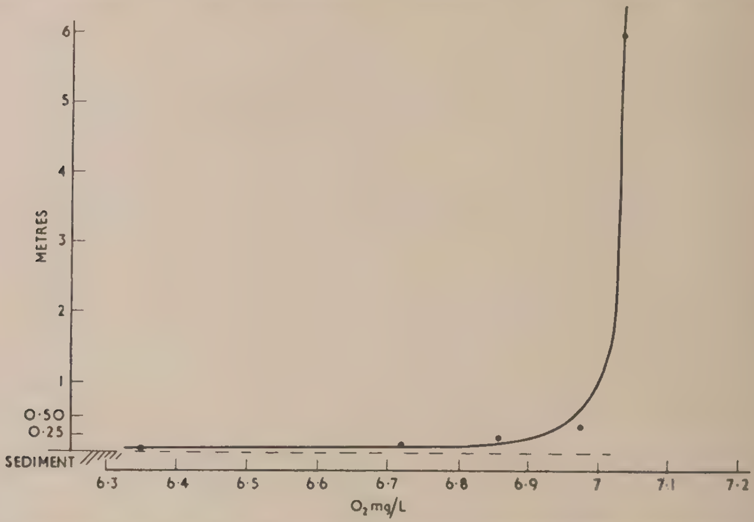

Fig. 6. Teneurs en O_2 de l'eau dans une couche de 6 m d'épaisseur au-dessus du sédiment (Préleveur de surface et Bouteille de prélévement).

Ainsi sont mises en évidence, d'une part, la très grande rapidité d'oxydation du sédiment et, d'autre part, l'extrême lenteur de diffusion du gaz dissous. Ce qui est de nature à expliquer que la chute rapide de la teneur en O_2 observée *in situ*, ne se produit qu'au proche voisinage du sédiment.

REFERENCES

BROUARDEL, J. et FAGE, L. (1953), Variation, en mer, de la teneur en oxygène dissous au proche voisinage des sédiments. *C.R. Acad. Sci., Paris*, 237, 1605–1606.

BROUARDEL, J. et FAGE, L. (1954), Variation de la teneur en oxygène de l'eau au proche voisinage des sédiments. *Deep-Sea Res.*, 1 (2), 86–94.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 45-57.

Foraminiferal faunas in cores offshore from the Mississippi Delta*

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Scripps Institution of Oceanography, La Jolla

Summary—Study of Foraminifera from fifteen cores shows presence of cold-water faunas interpreted as representing glacial stages and/or substages, and of warm-water faunas interpreted as post-glacial and interglacial stages and/or substages. These sequences are similar to those previously reported from the northwestern Gulf of Mexico.

The amount of post-glacial deposition is greater on the lower continental shelf and upper continental slope than on the lower slope and basin. Variations in amount of post-glacial sedimentation within these topographic provinces are demonstrated.

Two cores located in the bottom of Mississippi Canyon contain faunas and sediments which have been displaced downslope, presumably by turbidity currents. It is suggested that the turbidity current was confined to Mississippi Canyon, and that submarine canyons generally tend to localize many turbidity currents.

INTRODUCTION

Members of the Woods Hole Oceanographic Institution have pioneered in studies of the offshore sediments in the northern Gulf of Mexico. Extensive collections of surface sediments and longer cores were taken along 2,500 miles of traverses in the northwestern Gulf of Mexico in 1947, using the research vessel *Atlantis*. The physical parameters of these sediments were reported and interpreted by Stetson (1953), chemical studies of the materials are discussed by Trask (1953), and the foraminiferal faunas are described and interpreted by Phleger (1951) and Phleger and Parker (1951). In 1951 Stetson made extensive collections aboard the *Atlantis* in the northeastern area, from the Mississippi Delta to Florida, collecting surface sediment samples and long cores along several hundred miles of traverses. The foraminiferal facies in the surface sediments along these traverses have been interpreted by Parker (1954), and study of the sediments is being undertaken by Stetson.

The present paper is a study of the vertical sequences of foraminiferal faunas in fifteen of these cores in a traverse extending southward from the Mississippi Delta. The purposes of this study are:

(1) To discover whether there is a vertical sequence of cold- and warm-water faunas as reported from the western Gulf of Mexico and elsewhere;
(2) To attempt to discover relative rates of deposition off a large delta;
(3) To evaluate the role of turbidity currents in deposition in the area covered by the cores.

The cores were studied at the suggestion of Henry C. Stetson of the Woods Hole Oceanographic Institution, who furnished them to the writer. The assistance of Jean F. Peirson in this study is gratefully acknowledged. Dr. Rufus J. LeBlanc, of the Shell Development Company, kindly arranged to have several of the cores sampled. The laboratory work was supported by the Office of Naval Research (Project NR 081–050, Contract Nonr–233, Task 1).

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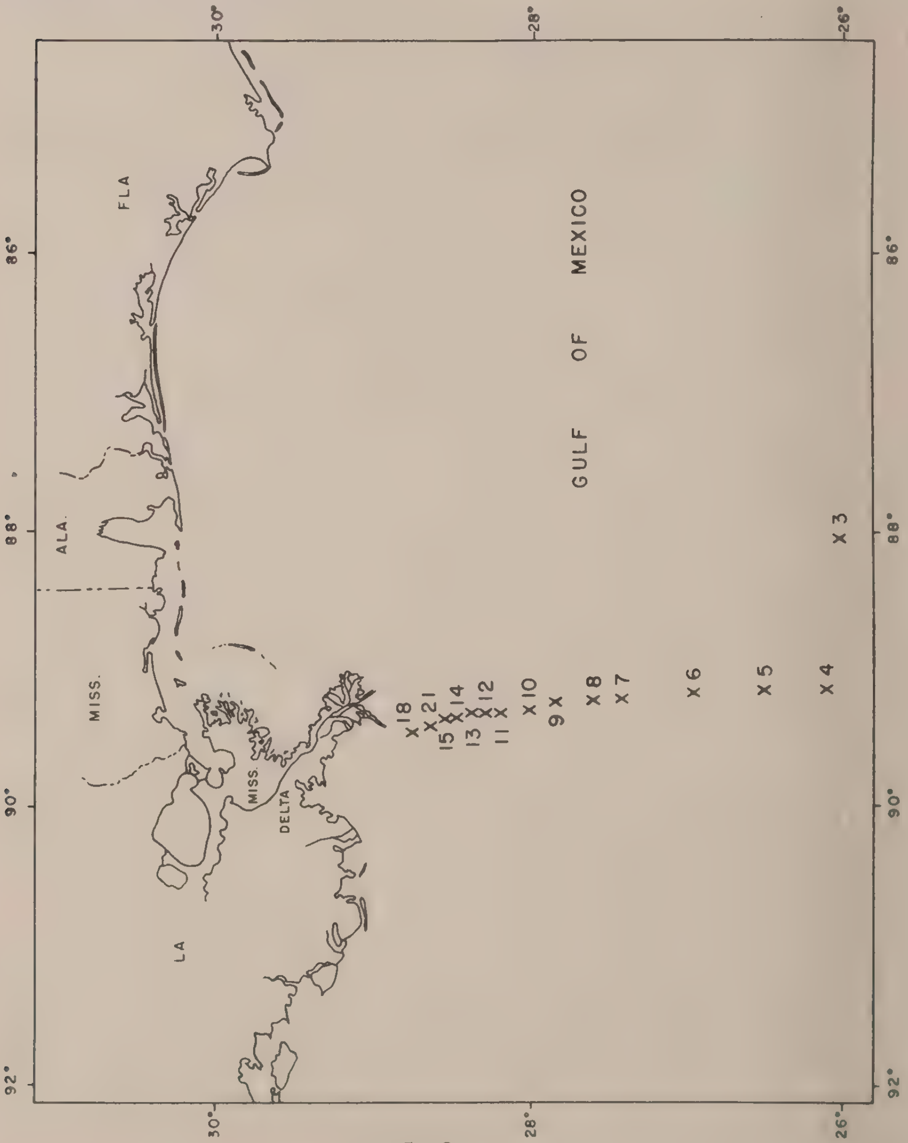
LOCATIONS OF STATIONS AND DESCRIPTION OF THE AREA

The cores were collected along a traverse (Table I, Fig. 1) extending from the deep Gulf of Mexico basin at 3,017 m to the lower continental shelf at 88 m. The near-shore, shallow end of the traverse is only a short distance off Southwest Pass, one of the main distributaries of the Mississippi Delta.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X 10
11 X
X 12
13 X
X 14
15 X
X 21
X 18

Fig. 1. Locations of cores in the Gulf of Mexico off the Mississippi River.

Table I—Locations and depths of cores

Core	*Depth in m*	*N. Lat.*	*W. Long.*
3	3017	26° 01′	88° 03′
4	2972	26° 07′	89° 09′
5	2788	26° 31′	89° 09·5′
6	2468	26° 58·5′	89° 12′
7	1875	27° 26′	89° 14′
8	1417	27° 37·5′	89° 14·5′
9	1372	27° 51′	89° 15′
10	1298	28° 01·5′	89° 19′
11	914	28° 12′	89° 20′
12	732	28° 18′	89° 20′
13	631	28° 23·5′	89° 20′
14	471	28° 29′	89° 22′
15	298	28° 33·5′	89° 22′
21	142	28° 39′	89° 25′
18	88	28° 45·5′	89° 27′

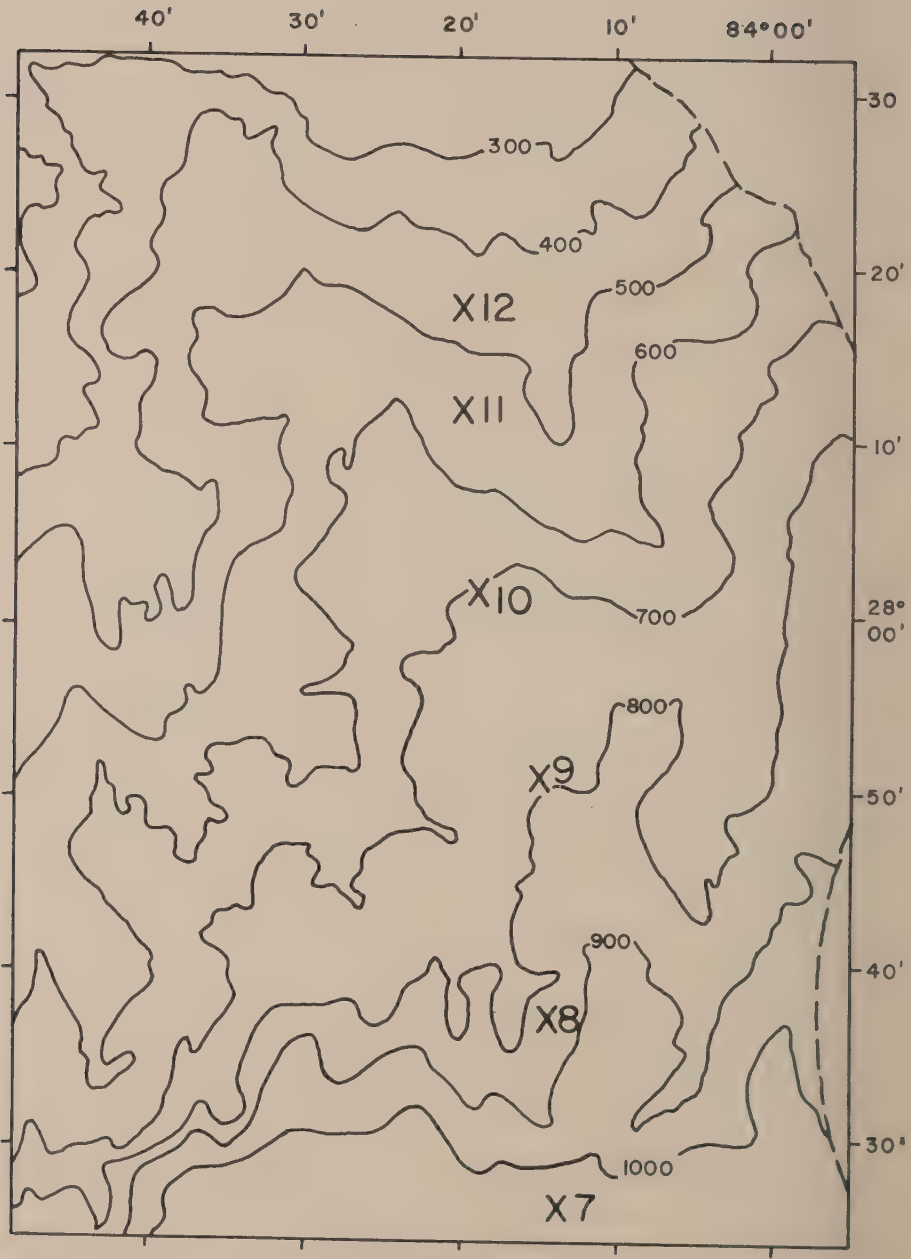
The topographic charts of the northwestern Gulf of Mexico, constructed by Gealy (1955), end at the approximate position of the Mississippi Delta, and all of the present core stations are off her chart except cores 7–12 (Fig. 2). Core 18 was taken at a depth of 88 m on the lower part of the narrow continental shelf. Most of the other cores came from the continental slope, except those at the outer end of the traverse which are in or on the edge of the Gulf of Mexico basin. The continental slope in this area appears to be quite rugged, and is cut by the Mississippi Canyon. The Sigsbee Deep Scarp described by Gealy may not be present in the area traversed by the cores.

This is an area of high runoff from the Mississippi River and is presumed to have a rather high rate of sedimentation. It has been shown by Scruton (MS.) that the highest sedimentation rate is close to the delta distributaries and decreases rapidly offshore. There appears to be rather rapid sedimentation for approximately 60 miles offshore, according to analyses by Phleger (MS.). It seems likely that sedimentation is more rapid farther offshore in this area than in any other part of the northern Gulf of Mexico.

The physical oceanography of the area is not well-known. Offshore surface temperatures vary from a mean minimum of 20° C in February to a mean maximum of 29° C in August, according to Fuglister (1947). It thus has the surface-water temperatures of North Atlantic mid-latitudes in winter and of low latitudes in summer. A considerable amount of low-latitude water enters the Strait of Yucatan, and while much or most of this flows out the Florida Strait, its effect may be pronounced in the area of the outer part of the present traverse. Offshore salinities in the Gulf of Mexico are approximately 36‰. A near-shore wedge of lower-salinity water is expected in this high runoff area. Parr (1935) shows salinities of approximately 24‰ in the upper 50 m a few miles to the east of the present traverse.

METHOD OF STUDY

The cores were collected with a coring tube described by Hvorslev and Stetson (1946). The samples used in the present study were one-fourth of each core cut into sections approximately 5 cm in length, so that the entire core was sampled. Each sample was trimmed of approximately 1/8 inch of sediment to prevent contamination between samples and was washed free of fine sediment over a brass sieve having an average opening of 0·074 mm.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X10
X9
X8
X7

Fig. 2. Locations of cores 7–12 in relation to topography. Topography modified after Gealy (1955). Depths in fathoms

The foraminiferal faunas were analyzed quantitatively. Only a fraction of the population was counted in samples having very large populations; quartering was done by a method described previously (PHLEGER, 1951, 7). Occurrences of species are listed in percent of the total; benthonic and

Table II—Occurrences of Foraminifera in cores 3–6, in percent of total population. Planktonic and benthonic populations computed separately

CORE	6																		
DEPTH IN METERS	2468																		
DEPTH IN CORE IN CM. FROM TOP	TOP	4-8.5	12.5-17.5	20-25.5	27.7-32.5	32.5-37.5	42-47	54-59	75-80	90-95	98.5-104	110-115	131-136	148-153	170-175	178-183	190-195	202.5-207.5	207.5-213.5
TOTAL PLANKTONIC POPULATION	52,000	98,000					140,000		1,700		16,000	2,800	510		90		12		
Globigerina bulloides	4	8					1		.2		10	4	2		8		8		
G digitata																			
G eggeri	7	12					12		14		9	9	14		2		8		
G inflata																			
G pachyderma													.4						
Globigerinella aequilateralis	5	4					4		1		2	.6	.4		1				
Globigerinita glutinata	3	1					3		2		6	3	8		6				
Globigerinoides conglobata	.5	.3					.5		.7		6	.8							
G rubra	45	23					23		29		51	43	55		49		43		
G sacculifera	17	31					40		31		5	27	4		26		25		
Globorotalia hirsuta																			
G menardii	5	8					3		5		.3	3					8		
G punctulata	1	4					1		1		7	3	3		2		8		
G scitula	1										.9		1						
G truncatulinoides	3	4					1		3			3	8		2				
G tumida	1	3					1		2			.3	.4		1				
Orbulina universa	3	3					7		6		2	.6	3						
Pulleniatina obliquiloculata	3	5					3		4		6	2	.8		3				
Sphaeroidinella dehiscens	.1	.5					.3		.2			.3							
TOTAL BENTHONIC POPULATION	550	1,000	1,700	1,700	2,500	1,800	1,100	56		17	530		76	210		14		7	5
Amphistegina (juvenile)																			
Angulogerina bella																			
Bolivina alata					.6	.9													
B albatrossi				.5		.4		2											
B lowmani		.8		.5	1	2	2				.2								
B paula		.8					2												
B pulchella primitiva	.4				.6														
B striatula spinata								2											
B subaenariensis mexicana	.4					.4							1						
B subspinescens	.4				.3		.8				1								
Bulimina spicata			.2	.5				4		6									
B striata mexicana	1	.8	1	.9	.6						.2								
Buliminella cf bassendorfensis				.5															
Cancris oblonga																			
Cassidulina subglobosa	6	5	4	5	2		2						1	.5					
Cassidulinoides tenuis	.4				1	.4							3			7			
Cibicides kullenbergi		1	1	1	3	2	2				2								
C robertsonianus	4	8	7	3	3	4	2	2		6	7			.5					
C wuellerstorfi	18	12	18	13	10	12	13	11		6	2		4	13		7		14	20
Eggerella bradyi	1	.4	1	.5	2	1	2			6	2								
Elphidium spp																			
Epistominella decorata	4	4	2	2	1	4	3	4		11	19		1	.5					
E exigua	.4	4	.2								.8								
Eponides polius	3	1	2	.5		.4					1			.5					
E tumidulus	.4	.8	1							19	.9		1	3					
E turgidus	4	2	3	1	2	9	2	4			13		7	27					
Globobulimina affinis & vars	5	12	8	11	14	15	15	9		6	18		48	44		7			
Gyroidina neosoldanii			2	9	6	.9					1								
G orbicularis	3		.5	5	1	1					1			.5					
Haplophragmoides bradyi	3		2																
Hoglundina elegans	4	14	14	30	28	25	4	28		11	10			1					
Karreriella bradyi																			
Lagenidae	6	8	5	6	7	7	4	4		6	2		5	1					
Miliolidae	.4	2	.2	2	.6	2	.8												
Nonion pompilioides	2	1	2	3	3	2	2	2			.2		3	.5					
Nonionella atlantica																			
N opima							2												
Plectina apicularis	.7		2																
Pseudoeponides umbonatus	3	3	3	3	3	3	3	2		11	1		8	2		50			
Pullenia spp	9	3	5	2	2	5	7	8			3			1					
Pyrgo murrhina		4	5	.9	.6	9	8				3		3	1					
Quinqueloculina sp		8		5		.9	.8	2			9								
Robulus spp			2			.4	8				.2		1						
"Rotalia" beccarii vars			2			.4													
"R" translucens			.2				2							.5					
Sigmoilina distorta																			
S schlumbergeri	4	2	1	2	.3	1		2			2			.5				29	
Siphonina bradyana																			
S pulchra																			
Siphotextularia rolshauseni																			
Triloculina tricarinata					.6		2												
Uvigerina peregrina	4	8	3	2	3	2	9			6	1		1	5					20
Valvulineria mexicana	2	[illegible]	[illegible]		2	2		4			3		8	2		29		57	40
Virgulina advena		4		9															
V complanata	.4				.3						6		4						20
V mexicana																			
V pontoni								2											
Latticarinina pauperata	3		2	.5	1	.6	2				6								
Other species	1	5	8	5	2	2	5	6		6	3		1						

CORE	5						
DEPTH IN METERS	2788						
DEPTH IN CORE IN CM. FROM TOP	TOP	8.5-14.5	44-49	71-76	109-114	134-139	167-172
TOTAL PLANKTONIC POPULATION	14,000	70,000	45,000	1,300	2,700	51,000	2,700
Globigerina bulloides	5	2	5	1	.9	4	.9
G digitata	.2						
G eggeri	5	7	9	12	11	11	11
G inflata							
G pachyderma							
Globigerinella aequilateralis	5	2	4	3	2	4	4
Globigerinita glutinata	12	17	15	11	8	24	17
Globigerinoides conglobata	.1	4	.3	.3	.3		
G rubra	46	36	27	34	37	32	44
G sacculifera	7	9	16	22	20	9	7
Globorotalia hirsuta							
G menardii	3	8	8	4	5	3	
G punctulata	.5	.7	1			2	5
G scitula	7		.3			.6	1
G truncatulinoides	2	4	3	2	2	2	2
G tumida	2	4	3	2	1	2	2
Orbulina universa	1	7	3	3	9	3	3
Pulleniatina obliquiloculata	2	2	4	4	3	3	4
Sphaeroidinella dehiscens			.7	.6	.3		
TOTAL BENTHONIC POPULATION	700	1,100	1,000	240	100	1,500	360
Amphistegina (juvenile)							
Angulogerina bella							
Bolivina alata		.7	.8		1	4	.3
B albatrossi							.3
B lowmani	2	3	5	6	2	2	.8
B paula			2		1	1	
B pulchella primitiva	.6					.5	
B striatula spinata			.4	.4			
B subaenariensis mexicana		.4	.8			.5	
B subspinescens	1	1	1		1	2	.3
Bulimina spicata							
B striata mexicana	.6						.3
Buliminella cf bassendorfensis			.4	.4	1	.3	.5
Cancris oblonga							
Cassidulina subglobosa	4	4	.4	.8	2	2	2
Cassidulinoides tenuis		.4	.8				.5
Cibicides kullenbergi			1			.3	
C robertsonianus	3	4	3	.4	1	3	.5
C wuellerstorfi	3	5	12	2	8	10	7
Eggerella bradyi		2	.4		1		.3
Elphidium spp		.7					
Epistominella decorata	20	9	8	2		14	11
E exigua	2	1	.8			.3	1
Eponides polius	8	6	2	.4		.8	
E tumidulus	3	5	2	.8		2	.8
E turgidus	12	8	7	9	18	9	14
Globobulimina affinis & vars	1	.4	4	50	5	9	36
Gyroidina neosoldanii		.4	.4			.3	
G orbicularis	1	2					.3
Haplophragmoides bradyi		2					
Hoglundina elegans	.6	4	13	6	31	4	6
Karreriella bradyi							
Lagenidae	10	11	12	9	15	12	4
Miliolidae	1		.4	2		.5	1
Nonion pompilioides	.6	2	5	.8	3	2	3
Nonionella atlantica			.4				
N opima							
Plectina apicularis							
Pseudoeponides umbonatus	1	2	.4	.4		2	3
Pullenia spp	4	7	2		1	.3	2
Pyrgo murrhina							1
Quinqueloculina sp	.6		.8			1	5
Robulus spp							
"Rotalia" beccarii vars							
"R" translucens						.3	
Sigmoilina distorta							
S schlumbergeri		7		.8		.3	.3
Siphonina bradyana				.4			
S pulchra							
Siphotextularia rolshauseni			4	.4		1	.5
Triloculina tricarinata	1		4	1		2	
Uvigerina peregrina						3	
Valvulineria mexicana	2		2	4		4	
Virgulina advena	6	2				.5	
V complanata	6	2	8	.8	3		
V mexicana	.6						
V pontoni			4				
Latticarinina pauperata	6	4	4				
Other species	5	3	7	4	6	5	2

CORE	4														
DEPTH IN METERS	2972														
DEPTH IN CORE IN CM. FROM TOP	TOP	0-5	11.5-15.5	23.5-28.5	31.5-36.5	47.5-52.5	57.5-62.5	82-87	110-115	120-125	148-153	160-165	165-170	170-175	181.5-186.5
TOTAL PLANKTONIC POPULATION	27,000	8,900		48,000		5,000	3,600	990	250						37
Globigerina bulloides	8					.8	1	2	.4						
G digitata	1														
G eggeri	10	7		12		11	7	4	20		X	X	X	X	8
G inflata		.3													
G pachyderma						.6	.3	.4	.4						
Globigerinella aequilateralis	5	3		1		.8	3	4	2						3
Globigerinita glutinata	9	10		10		10	8	3	6						
Globigerinoides conglobata	1	.3		.7			2	.4	.8						
G rubra	36	37		41		65	56	38	41		X	X	X	X	62
G sacculifera	9	16		18			8	38	10		X	X	X	X	8
Globorotalia hirsuta															
G menardii	4	4		4					.8		X	X			
G punctulata	.2	.6				2	7	.8	7		X	X	X	X	8
G scitula	4			.2			.3								
G truncatulinoides	2	7		2		.6	1	2	8		X	X			8
G tumida	2	6		2		3									3
Orbulina universa	5	4		5		4	4	.8	3		X	X			
Pulleniatina obliquiloculata	3	5		4		2	2	6	.4			X			
Sphaeroidinella dehiscens	.2					.6	.3								
TOTAL BENTHONIC POPULATION	510		570	1,000	600	400	140	150		220	40				23
Amphistegina (juvenile)															
Angulogerina bella															
Bolivina alata	.8				.3										
B albatrossi					.3										
B lowmani	.4		1	1	1	.2									
B paula	.4		1	.8	.3										
B pulchella primitiva	.4			.4											
B striatula spinata															
B subaenariensis mexicana				.4	1										
B subspinescens	1			.8											
Bulimina spicata															
B striata mexicana										.5					
Buliminella cf bassendorfensis					.3	.5									
Cancris oblonga															
Cassidulina subglobosa	3		2	3	.7	.5	.7	.7		.5	2				9
Cassidulinoides tenuis										1	20				53
Cibicides kullenbergi	.4		.7	.8		.2									
C robertsonianus	6		3	2	1	1	.7	1							
C wuellerstorfi	20		24	18	24	21	21	5		10	20				4
Eggerella bradyi	1		.7	.8	.3	2	3			.5					
Elphidium spp			.3	.4											
Epistominella decorata	8		8	4	10	2	6	.7		.5	2				
E exigua			.3												
Eponides polius	4		9	6	4	.2									
E tumidulus	6		5	9	3	3		4		2					
E turgidus	4		9	9	18	38	36	26		7	7				4
Globobulimina affinis & vars			10	3	7	2	5	50		55	36				9
Gyroidina neosoldanii			.3	.4		.2	1	.7		.5					
G orbicularis				.8	1	.5									
Haplophragmoides bradyi	2														
Hoglundina elegans	2		4	6	10	2		1							
Karreriella bradyi															
Lagenidae	2		7	7	6	2	4	2		3					
Miliolidae	.8		1	1	.3										
Nonion pompilioides	2		3	4	4	2	1	3		.5					
Nonionella atlantica															
N opima															
Plectina apicularis	3			1											
Pseudoeponides umbonatus	.4		2	8	2	5	9			3					
Pullenia spp	2		2	5	3	2	3	.7		.5					
Pyrgo murrhina			.3	2		5	.7	2							
Quinqueloculina sp					.3		3								
Robulus spp				.4											
"Rotalia" beccarii vars															
"R" translucens	8														
Sigmoilina distorta															
S schlumbergeri			.7	2	2		.7								4
Siphonina bradyana															
S pulchra															
Siphotextularia rolshauseni						5	7								
Triloculina tricarinata	4														
Uvigerina peregrina						2									
Valvulineria mexicana	.4			8	2	.6				3	.3				4
Virgulina advena	4														
V complanata	4		3		3		7								.3
V mexicana															
V pontoni															
Latticarinina pauperata				.4		.5									
Other species	26		4	8	3		2	2		1					

CORE	3										
DEPTH IN METERS	3017										
DEPTH IN CORE IN CM. FROM TOP	TOP	5-10.5	10.5-15.5	31.5-38.5	38.5-43.5	57-62	76-81.5	85-90	102.5-107.5	130.5-135.5	167-172
TOTAL PLANKTONIC POPULATION	63,000	56,000		68,000		32,000	3,000	1,400	2,100	960	
Globigerina bulloides	3	2		2		5	7	10	5	9	R
G digitata	.1										
G eggeri	6	7		8		10	11	11	9	10	
G inflata						.2		.3		.9	
G pachyderma						.4	4	1		4	
Globigerinella aequilateralis	4	6		5		2	6	6	3	1	
Globigerinita glutinata	13	5		4		12	8	7	13	8	A
Globigerinoides conglobata	.2	.9		.4			.9	1	.7	2	
G rubra	42	42		40		38	44	36	41	43	A
G sacculifera	9	15		26		16	7	9	17	6	A
Globorotalia hirsuta		.2				.2	.2	1	.4	.3	
G menardii	4	6		4		1			1		C-R
G punctulata	.1	.3		.2		3	3	8	.7	4	
G scitula	3	.6		.2		1		2		.3	
G truncatulinoides	2	2		.8		2	1		1	7	R
G tumida	.3	2		3		3	.2		.6		R
Orbulina universa	1	6		3		4	6	3	4	4	
Pulleniatina obliquiloculata	1	2		3		2	1	5	3	.9	
Sphaeroidinella dehiscens											
TOTAL BENTHONIC POPULATION	1,200		1,600	600	310	650	210		170	170	22
Amphistegina (juvenile)			.5		.6				.6		
Angulogerina bella				.7							
Bolivina alata	.3			.7							
B albatrossi											
B lowmani	4		2	12	3	1	.5		1		
B paula	1		1	.7	1	.6					
B pulchella primitiva	2		.5		1						
B striatula spinata											
B subaenariensis mexicana			.5	.7	1						
B subspinescens	1		.5	.7							
Bulimina spicata											
B striata mexicana	.3										
Buliminella cf bassendorfensis	.7					.3					
Cancris oblonga				.7							
Cassidulina subglobosa	2		2	5	5	2	1		.6	.6	10
Cassidulinoides tenuis	.3		.5			.3					
Cibicides kullenbergi				1							
C robertsonianus	.7			.7	.6	.9	.5		.6		
C wuellerstorfi	13		20	16	23	21	21		5	24	35
Eggerella bradyi	.3		.5	1	1	.3	1		2	.6	
Elphidium spp					.6	.6			1		
Epistominella decorata	21		20	9	4	14	3		5	2	5
E exigua	1					1					
Eponides polius	6		4	1	.6		1		.6		
E tumidulus	3		2	13	7	9	2		.6	5	9
E turgidus	6		7	5	4	13	31		38	18	9
Globobulimina affinis & vars			2		.6	4	11		5	28	5
Gyroidina neosoldanii			.5		3	.9	1		1		
G orbicularis											
Haplophragmoides bradyi	2		.5	.7							
Hoglundina elegans	3		8	5	9	5	3		2		
Karreriella bradyi											
Lagenidae	5		7	7	11	4	5		4	5	
Miliolidae	.6				1	1	2			1	
Nonion pompilioides	1		2	7	7	6	1		2	4	
Nonionella atlantica	.7					.3					
N opima											
Plectina apicularis	1										
Pseudoeponides umbonatus	1		2	.7	6	2	7		2		
Pullenia spp	.6		4	3	4	2	2		5	3	
Pyrgo murrhina	.3		1		2	9	2		6	.6	
Quinqueloculina sp					.6	9	5				
Robulus spp										.6	
"Rotalia" beccarii vars											5
"R" translucens	3		1				.5				
Sigmoilina distorta									.6		
S schlumbergeri	1		1	7	6	3			1		
Siphonina bradyana											
S pulchra	.3										
Siphotextularia rolshauseni	1		5				5				
Triloculina tricarinata	.7		5		6	6					
Uvigerina peregrina											
Valvulineria mexicana	.7				6				8	4	22
Virgulina advena			.5				5				
V complanata	1		.5		1	6	.5		1	2	
V mexicana	.7			1		.3					
V pontoni											
Latticarinina pauperata	.3		5			3			1		
Other species	6		7	6	5	7	3		5	2	

Table III—Occurrences of Foraminifera in cores 7–11, in percent of total population. Planktonic and benthonic populations computed separately

CORE	11								10						9									8										7							
DEPTH IN METERS	914								1298						1372									1417										1875							
DEPTH IN CORE IN CM. FROM TOP	TOP	5-105	62-675	133-1385	170-1755	190-195	203-209	2215-227	TOP	25-7	235-285	565-615	105-110	144-155	TOP	3-8	.95-145	145-195	36-41	545-595	735-785	119-124	158-163	TOP	9-14	35-40	55-60	84 89	89 94	1035-1085	1115-1155	1155 1195	1385-144	TOP	0-5	115-17	155-255	30-35	52-57	95-100	120-125
TOTAL PLANKTONIC POPULATION		3,700	2,700	12,000	9,500	5,200	2,100		1,700	2,300	4,000	900	600		5,300	3,100			6,700		3,200	97	31	7,000	170	180	120	120			2,600			100,000	57,000			28,000	3,400	65	9,200
Globigerina bulloides			4	4	8	4	6		6	2	.4	.9	2		9	1			.5		2	1	13	6		2		.8			2			3	1			4	3	3	5
G eggeri		14	8	19	16	19	11		14	13	14	8	16		10	12			14		11	4	6	18	10	10	8	14			20			8	10			11	9	15	9
G. pachyderma							1																																		
Globigerinella aequilateralis			1	2	.7				4	.3	.8		1		6				2		.7		3	3	2	3	.8	2			1			7	2			4	5	6	1
Globigerinita glutinata		3	6	7	5	2	7		3	4	4	6	3		5	3			4		5	10	10	1	.6	3		6			2			2	2			6	6	8	8
Globigerinoides conglobata		.4	.3			.5	.6		2	.3	2	.4				3			2		.2			3	.6									.5				.3			.3
G rubra		33	37	35	45	48	41		25	25	27	39	31		32	27			33		35	51	33	23	29	22	43	35			33			32	41			35	38	24	36
G sacculifera		17	12	13	8	8	8		6	10	14	13	19		5	13			12		12	8	10	6	36	35	25	6			14			15	17			11	20	24	17
Globorotalia menardii		11	8	.6	X	X	X		9	13	13	8	8		3	13			9		11	7	6	9	7	9	3	7			.3			11	8			9	4	2	.3
G punctulata		2	5	4	6	11	10		1	2	.4				.6	2					2	1	3	.7							13			.4	1			1	.3		14
G scitula			.3				.6		2						2						.2													.5							.8
G truncatulinoides		6	8	4	2	4	5		13	11	12	9	7		7	12			9		10	6	3	12	5	5	4	4			3			5	5			7	2	6	3
G tumida		2	1	2	3	.5	4		3	3	3	5	2		2	4			2		1	1		4	6	1	3				3			2	2			2	.9	5	2
Orbulina universa		9	.9	3	1	1	2		3	4	.8	3	2		8	2			1		3	7		2	7	5	5	10			3			8	4			5	6	2	2
Pulleniatina obliquiloculata		10	8	5	5	2	4		9	12	9	7	8		10	8			11		7	4	13	12	2	5	7	11			5			4	7			4	5	2	2
Sphaeroidinella dehiscens		.4	.3																								.8	2						.2					.3	3	
TOTAL BENTHONIC POPULATION	160	2,100	1,200	2,800	3,700		3,200	530	320	390	830	280		120	380	460	370	780	[illegible]60	340	410	30	160	430	[illegible]2		170	200	170	160	250	400	290	180		200	42		280		
Angulogerina bella																							.6																		
Anomalinoides mexicana			.3	.1	.3		.1				.2	.7			.3		.5	.1	.2									1	6		.4	2									
Bolivina alata							.1			4		.4		.9		.7	2	.1		3	17		3	2	50		63	12	17	42	30	33	45				32		46		
B albatrossi	3	12	10	.7	1		1		8	11	10	7		.9	.8	4	8	2	5	5	6	3	1	3	2		1	1	2	7			.3	4		1	2		2		
B barbata														3									4																		
B lowmani		1	2	2	.1		.1		2	2	3	.7		7	1	1	2	2	1	.9	1		2	.2	1					1	.4								.7		
B ordinaria		2	2	7	6		12	5		.5	.7					.2			.2	1					1			5		.6									.4		
B pulchella primitiva														.9																			3								
B striatula spinata														5		.4				.3	.5		4									.2									
B subaenariensis mexicana		.2					2	4						2									4	.2	6		.6	1		.6		.2	.7				2		2		
Bulimina aculeata	4	3	1	6	21		16	8	11	15	18	10			13	21	15	10	21	23	16	14	1	2							1	1	1	7		9					
B alazanensis		6	5	1	2		3		5	4	3	3			1	1	1	2	2	3	2			2					1		2	3				.5					
B marginata														5									2																		
B spicata		2	2	.9					4	.8	2	3			1	.7	.3	.4	.9	.3	2	3	.6	2				.5						2							
B striata mexicana		.2	.5		2		2	3	.6	2	.4					.7		.8	.5	1				.9	1			4	4		8	2	.3	.6		1			7		
Buliminella cf. bassendorfensis										1		2		13		.2				.3	1	7	5										1			.5			.4		
Cassidulina carinata		.6	.3	1	4		20	73						.9		.2	.3		.2		.5	20	20				2	.5		1	1	1	.7				2		1		
C subglobosa		9	4	10	5		5		2	9	11	13			4	5	4	6	5	6	4	3		4	1		.6	1	.6	2	3	7	1	11		3			.4		
Chilostomella oolina		.2		.1			.1		.9	.3						.4					1	7	1				22	.5		4	1	.5	16						.4		
Cibicides aff floridanus	.6	2	5	4	3		.8	.2	4	5	5	5			3	3	2	2	3	3	1	3		4							.4										
C robertsonianus			2	.1			.1		2	.5	1	2			.8	1	2	2	3	.6	1			.2				.5	.6		2	3		5		3					
C wuellerstorfi		.2	.2	.1	.3				.9	1	2	1			.8	5	4	2	2	4	3			2	1			1	3		2	2	.7	3		7					
Cibicidina strattoni														2																											
Elphidium spp														4									1										.3								
Epistominella decorata									.3						3	1	2	3	1	.6				2	4			1	4	2	8	5	3	18		1			10		
E exigua		4	5	12	11		3	.2	4	2	4	4		2	1	1	3	2	3	2	2	7		.5	2		.6	3	1	6	.8	.2	2	3		.5			1		
E rugosa		2	.8	.9	1		.5					.4					.5	.1		.6	.5																				
E vitrea														27									19																		
Eponides polius		.4	.2	.7						.8	1	1		.9	.3		2	.5	1	.3	1									.6	.8	.2									
E tumidulus											.8				.3	.9	.3	2	.2		.2								.6					2		1					
E turgidus		8	5	4	2		5		.6	3	5	3			6	7	8	10	21	12	3			.9				1	2	.6	3	1	.7	.6		3	10		5		
Globobulimina affinis & vars	.6	.6	2	.4	.9		.5		3	2	.5	1		2		4	.8	.1	1	2	2				23		2	30	35	1	10	8	2	2		15	34		14		
G mississippiensis																							2																		
Gyroidina orbicularis		3	.8	.6	1		1		2	1	2	4			2	3	4	5	4	2	3			4				2	.6		1	1	7	5		3					
Haplophragmoides bradyi	7								1	.3					.5	2		2						.9										3		.5					
Hoglundina elegans		.7	.2	.3	.2		.1			.8	.7	.4				3	4	2	1	2	.7										4	2		6		11	5				
Lagenidae		2	2	4	3		.3	1	.3	5	4	9			3	4	4	6	4	3	6	7		.7	2			4	1	4	3	2	3	3		4			3		
Loticarinina pauperata		2	.6	1	1		.3		.9	2	2	2			1	2	2	2	1	2	2			.9							2	3		1		2	2				
Miliolidae		.8	2	.6	.5		.2		2	.9	2	.4		5	1	1	1	1	.4	1	1	3	1	9					.6		2	4	3	1					.4		
Nonionella atlantica																																		6							
N opima														6							.2		1										.7								
Osangularia cultur	.6	7	13	.7					2	3	2	6			.8	3	1	2	3	2	3			3	1		1	5	4	3	1	2	.3	2		3	2		.7		
Pseudoeponides umbonatus			.5	.1	.3		.1		.3	.5	2	.4			.5	1	1	.3	.5	.3	.5							3	4	1	4	7		.5		1			.4		
Pullenia spp.	.6	2	1	1	1		.2		4	2	3	2			1	3	5	3	4	5	2			.9				2	3	.6	2	1	.3	1		4			.4		
Rectobolivina advena																							.6																		
Robulus spp		.2			.3				.3		.6			2		.2	1	.5	9		.2		2	.7				1	2	1	4	2	.7	.6		5					
"Rotalia" beccarii vars														4									4																		
"R" translucens		1	3	3	13		12	.2	3	5	1	5			.3	.9	2	6	.2	2	3	3	.6							1				.5							
Uvigerina parvula														3									8																		
U peregrina	1	14	21	22	10		5	.2	6	7	8	5			6	8	8	4	5	4	6			15	2			17	8	5	5	6	3	5		15	2		5		
Virgulina mexicana					.1		.5	7								.2					3	20	3				2	.5	1		.4	.7	6						.4		
V pontoni														2									2																		
V tessellata		2	.6		.1		.3		3	.5	4	7				.2	.3		.2	.3	.2																				
Other species	82	3	8	16	10		9	2	29	8	6	8		2	48	10	9	24	4	10	4		8	47	3		5	7	4	5	12	10	7	.2		9	7		5		

Table IV—Occurrences of Foraminifera in cores 12–15, 18 and 21, in percent of total population. Planktonic and benthonic populations computed separately

CORE	18						21						15								14						13						12							
DEPTH IN METERS	88						142						298								471						631						732							
DEPTH IN CORE IN CM FROM TOP	TOP	4-9	45-50	99-104	124-129	162-168	TOP	15-20	44-49.5	74.5-80.5	120-125	192-198.5	TOP	13-19	42-47	55-60	86-91.5	117-122.5	163.5-170	192-197	TOP	4.5-10	48.5-53.5	90-95	124-129.5	180-185	TOP	7.5-13	45-50	86-91	134-139	174-180	TOP	15-20	67-72	85-90	109-114	153-155	170-175	200-205
TOTAL PLANKTONIC POPULATION	3	6	18	8	1	10	0	97	300	140	280	12,000	300	1,700	2,300	24,000	900	170	23		2	9,200	270	16,000	26,000	19,000	7	150	200	850	1,100	5,000	75	250	500	500	2,200	2,500	3,600	11,500
Globigerina bulloides	67							8	4	6	1	1	3	4	3	4	3	3	13			6	3	6	6	16		.7	2	5	4	7	4	5	7	3	1	6	2	7
G. eggeri			22	12				14	15	13	11	10	27	10	12	12	12	12	4			11	15	11	12	11		13	7	7	14	9	20	14	11	9	13	14	17	20
G. pachyderma																										2														2
Globigerinella aequilateralis						10		1	2			2	.4	1		1	.4	2				1	3	.6	.6	.8		1	.5	1	.7	2		.4	.4	.4	.7		1	.6
Globigerinita glutinata			11		100			6	3	2	7	6	5	2	3	1	3	1				2	2		8	7		5	3	1	4	6	3	.8	2	3	3	3	.9	2
Globigerinoides conglobata								3		2	.7	.6	.7	2		1	.9					.3	2	2	3	.8		1	.5	2	.4	1		1	.8	.4	.4		.4	
G. rubra	33	50	27	40		20		44	28	43	35	42	12	38	42	51	40	54	62		100	44	28	39	37	48		27	30	34	29	38		36	35	30	28	41	38	32
G. sacculifera		33	6	12		10		4	10	8	12	6	4	16	13	13	18	16	13			8	5	9	17	3		9	12	11	7	10		6	4	10	11	14	21	9
Globorotalia hirsuta													.4	3	2	3	.7	2												.4										
G. menardii		17		12				1	7	3	14	10	13	3	2	4	5	3				6	9	8	6		14	11	12	16	12	9		5	3	11	14	4	5	.3
G. punctulata								1	.7				.7		.7	1	.4	.6				.7	.7	.6	.3	5	14	3				.3	3	.4			5		.2	10
G. scitula																									.3	2														
G. truncatulinoides			22			30		9	8	3	4	7	12	10	11	3	6	3				10	11	7	4	.5	29	15	18	9	9	7	43	9	7	8	8	4	4	4
G. tumida									3	2	1	1	6	6	4	1	1	1				3	4	2	1			.7	4	3	7	3	4	3	6		5	5	2	6
Orbulina universa			6	12				3	5	5	3	3	1		.4	.7	2		4			2	7	3	1	3		1	1	.7	4	.6	3	3	5	7	2	3	2	1
Pulleniatina obliquiloculata			6	12		30		6	14	13	11	11	14	5	7	4	8	2	4			6	10	12	3	1	43	12	10	10	13	6	20	14	19	17	9	6	6	6
Sphaeroidinella dehiscens																							.4		.6					.4						.4			.2	.3
TOTAL BENTHONIC POPULATION	250	1,200	2,800	1,400	1,100	950	120	4,600	3,900	5,600	4,200	15,000	800	3,500	2,800		1,300	1,300	1,300	1,100	36	5,200	1,800	6,700	6,400	10,000	250	750	800	1,400	1,900	3,400	410	1,000	1,000		1,300			7,100
Ammoscalaria pseudospiralis	.4	3	.6	2	1	2	8																																	
Bolivina albatrossi									.4	.6		1	9	11	14		12	2				6	2	4	9	11	3	5	4	7	7	8	6	5	10		10			1
B. barbata		13	3	3	3	3		15	12	15	8	.9	1	2	.9		.6	4	2	6								.5												
B. lowmani	.4	.3	.3	.3	.4			1	2	8	2	1	.7	1	2		.6	.5		.4			.9	.5	1	.3		2	.5	.6	1	2	1	.8	.4		.9			
B. ordinaria								2	1	3	3	3	3	3	5		4	1	2	.7		13	14	8	9	11	11	10	6	13	18	15	7	3	4		10			14
B. striatula spinata		4	2		.4	2		.3		.3												.6																		
B. subaenariensis mexicana		1	.9	.6	1	2		40	21	15	13	6	.7	11	5		9	13	13	9		.6		1	1	5				1		.5		.2	.8		.3			
B. subspinescens									.8		.4	3	1	1	.3				.3			.6			1	3	.4		1	1	.8	.9	1	.4	.2		.6			.6
Bulimina aculeata																						.6					14	5	2	.6			2	4	.4		.5			12
B. alazanensis																						3	.9	2				3	1	4	3	4		4	5		9			3
B. marginata		15	8	4	9	5		20	15	6	8	12	13	3	4		10	23	22	31		.6		2	2	1														
B. spicata													1											1	.3	.3	4						.7	1	1		1			.1
B. striata mexicana									1	.3	.4	.4	12	5	4		2	1	1	.7		3	6	4	.5	.3	13	4	5	4	2	2	5	6	3		1			.7
Buliminella cf. bassendorfensis		32	17	30	22	34			.2	3																		1												
Cassidulina carinata								.2	1					3	3		3	1		.7		4	30	10	5	2		17	49	6	3	2		13	2		.9			9
C. curvata								.5	2	3	2	2	2	2	2		3	.5	2			7		2	1	2	.4				.4									
C. neocarinata								.5	1	4	6	6	.7	3	4		2	1	2				3	1	2	2	.8	.5			.4		.2							1
C. subglobosa			.6					.3	.4	3	3	1		3	1		.9	.3	1	.4		2	.4	5	1	1		8	3	6	9	8	.2	4	8		11			17
Cibicides aff. floridanus		.3						2	15	9	16	9	4	11	9		11	3				.6	3	2	1	2	4	2	1	3	3	4	3	5	8		5			2
Elphidium spp		.3											.7				.3																							
Epistominella exigua														.2								1		1			7	7	4	12	15	19	4	5	5		6			2
E. rugosa														.2			.3						.4	2	3	5						.9		2	1		.9			.5
E. vitrea	.4	16	31	30	42	23		.3	.4	3	1								.3			.6																		
Eponides regularis								6	8	6	6	1	2	4	.9		7	37	34	36		.6	.9	1	.7	1	2													.1
E. turgidus																						2		.5			4	3	2	6	2	.9	.5	.6	5		3			8
Globobulimina affinis											5	.4	.2														.4	.5			2		2	1	1		1			.2
G. mississippiensis		7	.3	1	2	.4		2	1										.3																					
Gyroidina orbicularis													.2				.3					.6	2			.3					2	.5		.4	2		2			.6
Gyroidinoides altiformis									.6		.8			.5	.9		.3	2	2			.6	.9	.5	.5	2			.5	.6	.4	.9		.2	.4		.2			1
Goesella mississippiensis	3						53														3																			
Lagenidae		.2	.3					1	1		2	2	2	1	.9		.9		2	2		2	1	1	2	2	.4	2	2	1	1	3	1	1	1		1			1
Miliolidae			1	.6		.9		.4	1	2	1	1													2	9		.5			.8	.5		.2						.2
Nonionella atlantica		7		.3																							.4													
N. opima			.3	.3	.4			1	1		.4		.2				.6																							
Osangularia cultur																											.4	2		4	2		5	6	6		3			
Planulina ariminensis															.3							1		3	3	.3						2		.2			.3			.6
P. foveolata									1	.6	3	3	.2	.5	2		2	.6				1																		
Pullenia spp									.6		1	.4	.7	1	.9		1	.2				3	1	2	1	.6	.4	2		.6	1	1		.2	.4		.3			.8
Rectobolivina dimorpha																								.5								.5								
Rotalia spp		4	.6	.8	4			.3	1	1	3	3	3	3	4		3	.6					1	1	1	9			.5	.6					.2		.3			.3
Rotalia translucens													.2	3	4		2	5	11	7		14	17	14	21	27		6	4	10	8	7		10	11					12
Rotamorphina laevigata								.2				2														.6	.4	1			2	.9	.2	1	.8		1			1
Sigmoilina distorta								.7	.8	3	.8	2		.2										.5	.3															
Siphonina pulchra									2	.3		3					.3							1	1															
Sphaeroidina bulloides								.2	1	.6		2	8	4	3		2	.3	.9	1		6	4	5	7	3	8	2	2	3	5	2	6	6	4		5			.8
Textularia earlandi	61						9														11						2						9							
Trifarina bradyi																						.6		1	7						.4				.6		.2			.2
Uvigerina laevis								7	2	3	[illegible]	9			.3		.6		9					5		9														
U. parvula		6	33	27	18	26		2	4	3	8	7		.9			12	2	3																					
U. peregrina													16	16	25		5	.3				7	1	14	1	7	6	7	7	8	5	6	12	2	3		16			4
Valvulineria mexicana		.3	.3					.2	.2	.9		.4	4	9	6			.3	6	4		6	2				2		1				2	.2	4					
Virgulina mexicana														5	.3									5			.4	.5	5	6	8	.5		.2	.2		.2			
V. tessellata																									.3							9	2		.2					.3
Other species	35	3	1			2	38	3	3	8	3	19	13	3	3		4	1	3	5	86	8	9	9	12	6	16	9	4	8	5	7	30	7	5		8			6

planktonic forms are treated as separate populations, with each constituting 100%. Total populations are estimated for each sample, since they all contained approximately the same amount of sediment, with a few exceptions. Results of the faunal analyses are on Tables II–IV. Only the more common and/or important species are included in these lists; detailed analyses are on file at the Marine Foraminifera Laboratory.

Detailed faunal analyses were made on only a few samples from each core, but each sample was examined to ascertain whether or not there was a faunal change. Faunas in surface sediment samples from the stations along this traverse, collected with a small coring tube, have been analyzed by PARKER (1954). Population data from some of these samples are included for comparative purposes, since the top sample from a long core may not represent the actual surface sediment due to methods of collecting and processing.

The following should be consulted for illustrations, descriptions, and additional distributions of the species listed in the present report: PHLEGER and PARKER (1951), PARKER (1954), PHLEGER, PARKER and PEIRSON (1953), and PHLEGER (1954).

CORE FAUNAS

In a previous study of core faunas from the northwestern Gulf of Mexico (PHLEGER, 1951) it was possible to differentiate an " upper " and " lower " core fauna based on the assemblages of planktonic Foraminifera. The upper planktonic fauna is the modern one and has the following general composition:

30–70%
    Globigerinoides rubra (d'Orbigny)

10–20%
    Globigerina bulloides d'Orbigny
    G. eggeri Rhumbler
    Globorotalia truncatulinoides (d'Orbigny)
    Pulleniatina obliquiloculata (Parker and Jones)

5–10%
    Globigerinoides sacculifera (H. B. Brady)
    Globorotalia menardii (d'Orbigny)

<1–5%
    Globigerinella aequilateralis (H. B. Brady)
    Globigerinoides conglobata (H. B. Brady)
    Globorotalia tumida (H. B. Brady)
    Orbulina universa d'Orbigny

The planktonic fauna which is widespread in lower sections of most northwestern Gulf of Mexico cores differs in having many or all of the following species absent or lower in frequency:

Globigerina eggeri Rhumbler
Globigerinella aequilateralis (H. B. Brady)
Globigerinoides conglobata (H. B. Brady)
Globorotalia menardii (d'Orbigny)
G. truncatulinoides (d'Orbigny)
G. tumida (H. B. Brady)
Orbulina universa d'Orbigny
Pulleniatina obliquiloculata (Parker and Jones)

In addition, the following occur in the lower fauna:

Globigerina inflata d'Orbigny
G. pachyderma (Ehrenberg)
Globorotalia punctulata (d'Orbigny)
G. scitula (H. B. Brady)

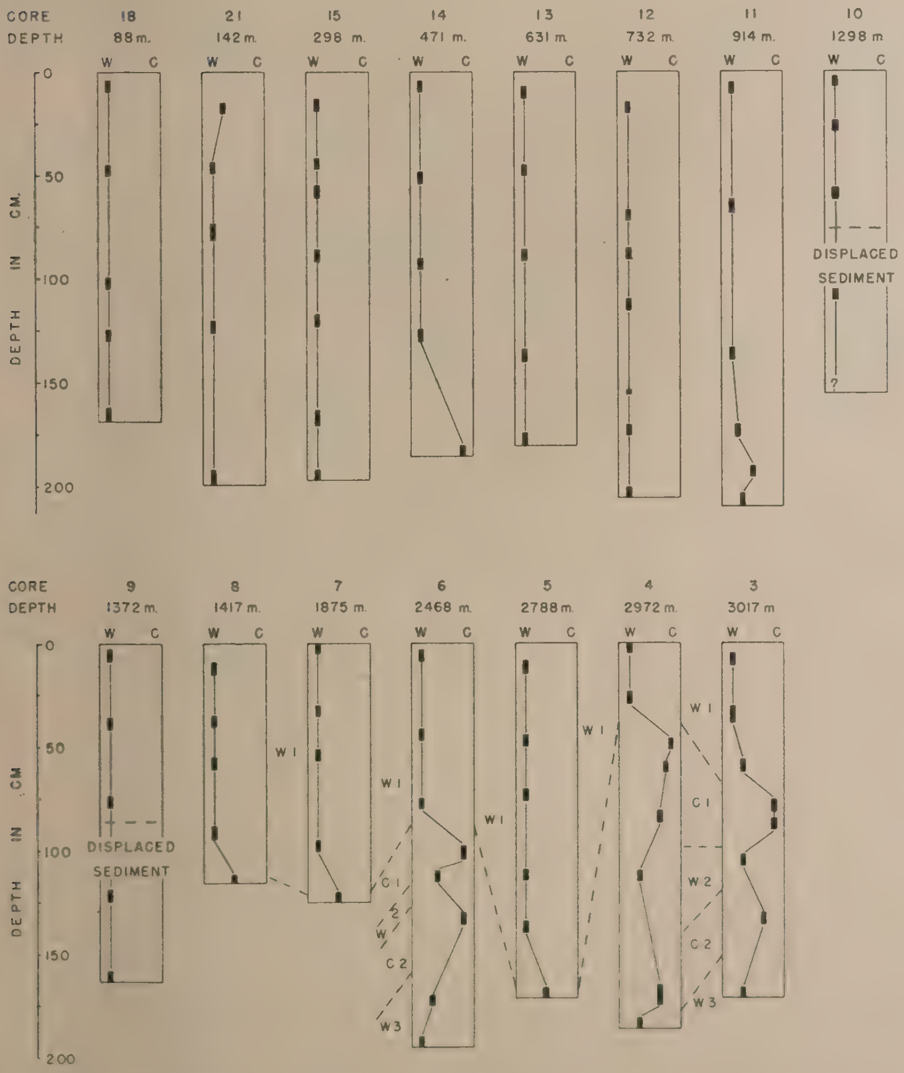

Fig. 3 Relative temperatures indicated by Foraminifera in the cores. W, relatively warm surface water. C, relatively cold surface water

The present cores contain " upper " and " lower " faunas which are comparable in species composition to those previously reported, with the following exceptions: in the upper, modern assemblage *Globigerinoides sacculifera* generally is more abundant especially in the area farthest off shore, *Globorotalia truncatulinoides* may be less abundant, and *Globigerina eggeri* may be more abundant; in the lower fauna, *G. inflata* and *G. pachyderma* are less common, being recorded in very low frequencies from only occasional samples.

The " upper " planktonic core fauna contains the modern assemblage and is assumed to represent conditions similar to those obtaining today, and may be considered to represent relatively warm surface water. The " lower " fauna contains fewer North Atlantic low-latitude planktonic specimens and consequently more mid-latitude forms, and is considered to represent a time of cooler surface water. Interpretation of these distributions may be clarified by examination of the data and discussion in PHLEGER *et al.* (1953) on distributions of North Atlantic planktonic Foraminifera.

Lower, colder-water faunas were present in eight of the fifteen cores examined. The interpretations of the faunas are summarized in Fig. 3, and the faunas on which these interpretations are based are listed in Tables II–IV. Cores 3, 4 and 6 contain two cold-water faunas separated by a warm-water fauna and their lower sections contain an additional warm-water fauna. Cores 5, 7, 8, 11 and 14 contain a cold-water fauna in their lowermost sections. The other cores contain the modern Gulf of Mexico planktonic fauna throughout their entire lengths. Core 18, on the lower continental shelf at a depth of 88 m, contains few planktonic specimens.

The benthonic Foraminifera in most of the core samples are normal for the water depths at which the cores were collected (see PHLEGER, 1951, Figs. 22–25; PARKER, 1954, Figs. 3–9). Striking exceptions occur in cores 9 and 10. In core 9, from 1372 m depth, the bottom sample at 158–163 cm contains the following shallow-water (continental shelf) species in significant frequencies:

Angulogerina bella Phleger and Parker
Bolivina barbata Phleger and Parker
B. striatula spinata Cushman
Bulimina marginata d'Orbigny
Buliminella cf. *bassendorfensis* Cushman and Parker
Elphidium spp.
Globobulimina mississippiensis F. L. Parker
Nonionella opima Cushman
Rectobolivina advena (Cushman)
" *Rotalia* " *beccarii* (Linné) variants
Virgulina pontoni Cushman

A few of these species occur in lower frequencies from 145–158 cm, and single specimens of *Bolivina striatula spinata*, *Buliminella* cf. *bassendorfensis* and *Liebusella* sp. occur at 3–8 cm in the core. Most of the benthonic Foraminifera in this core are normal for the depth at which the core was collected. Quartz grains of fine sand size and wood fibres which are coloured dark brown occur from 85 cm to the bottom of the core.

In core 10 from a depth of 1,298 m the following shallow-water species are important constituents of the bottom core section at 144–155 cm:

Bolivina pulchella primitiva Cushman
B. striatula spinata Cushman
Bulimina marginata d'Orbigny
Buliminella cf. *bassendorfensis* Cushman and Parker
Cibicidina strattoni (Applin)
Elphidium spp.
Nonionella opima Cushman
" *Rotalia* " *beccarii* (Linné) variants
Virgulina pontoni Cushman

A few specimens of *Buliminella* cf. *bassendorfensis* also occur at 56·5–61·5 cm and 2·5–7 cm. Plant fibres and fine quartz sand occur in the samples from 75 cm to 155 cm. The major part of the benthonic fauna consists of species normal for the depth of the core.

Twenty-six specimens of *Gümbelina* are recorded from the lowermost section of core 10.

Occasional shallow-water benthonic Foraminifera are recorded from the following additional deep-water cores of this series: 3, 4, 5, 6, 7, 8, 13 and 14. These are single specimens and no sample contains more than four specimens, while many contain none. No other evidence of displacement of sediment was observed.

DISCUSSION

Interpretations of the core planktonic Foraminifera in terms of " warm " (like the present) and " cold " (colder than present) surface water temperatures are given on Fig. 3. In this figure, " W 1 " refers to the modern warm-water fauna, " C 1 " to the last cold-water fauna, " W 2 " to the preceding warm-water fauna, etc. It is suggested that these stages can be correlated in the present cores, as shown on Fig. 3, especially where a succession of such faunal variations occurs and where there is no indication of displaced sediment. This is especially striking in comparing cores 3, 4 and 6. These cores came from the same relatively small area and from similar depths in the eastern Gulf of Mexico basin. Each of them has three warm-water faunas separated by two cold-water ones, and these occur within approximately the same thickness of sediment.

It is suggested that these warm and cold faunas also are to be correlated with similar successions described previously from northwestern Gulf of Mexico cores (PHLEGER, 1951, Figs. 29–33). The cold-water faunas have been interpreted elsewhere as representing Pleistocene glacial stages and or substages and the warm-water faunas are thus possible interglacial stages and or substages. The widespread occurrence of a cold-water fauna beneath the modern fauna in this region suggests a general cooling of Gulf of Mexico surface water during the last glacial or stadial stage.

Correlation of the planktonic faunas makes it possible to estimate the amount of post-glacial sedimentation along this traverse. This is based on the assumption that the upper, warm-water fauna represents post-glacial deposition. The amounts of deposition appear to be approximately as follows:

Core	*Water depth in m*	*Estimated post-glacial deposition in cm*
3	3017	65
4	2972	40
5	2788	170
6	2468	90
7	1875	120
8	1417	115
9	1372	>150
10	1298	>150
11	914	>210
12	732	>205
13	631	>180
14	471	155
15	298	>195
21	142	>195
18	88	>165

Some useful generalizations may be made from these data. The amount of post-glacial deposition is smallest away from the major source of supply, the Mississippi River, and near the centre of the basin; there is a general increase in amount of deposition closer to the source, as expected. In all but one core shoaler than 1,400 m the coring tube did not penetrate through post-glacial sediment. There is considerable local variation in the amount of post-glacial deposition. For example, in core 5 in the basin there is two to four times as much post-glacial deposition as in nearby cores from similar depths. Core 14 on the upper part of the continental slope has considerably less post-glacial sedimentation than nearby cores at similar depths and position. The amount of post-glacial deposition in the cores from the basin and lower continental slope in the present cores is comparable to that shown in cores from the basin and lower slope reported previously from the northwestern area (see PHLEGER, 1951, Figs. 29–33). The amount of such deposition on the upper slope appears to be larger than in the western area, although there are exceptions.

Cores 9 and 10 contain sediments and faunas in their lower sections which appear to have been displaced downslope from shoaler depths, presumably in the form of turbidity currents. The presence of abundant sand, wood fibres and abundant shallow-water benthonic Foraminifera at water depths of 1,298 m and 1,372 m appears to be conclusive evidence for such displacement. Most of the benthonic Foraminifera are species normal for the depth at which the core was taken; this demonstrates that the displaced material was deposited at the present water depths at those stations. The age of the displacement is post-glacial (W 1), as shown on Fig. 3.

Cores 9 and 10 occur in the bottom of Mississippi Canyon (Fig. 2). Other cores in this traverse do not have displaced sediment, at least in significant amounts, and these are located on topography other than the canyon floor. This suggests that the turbidity flow was localized in the canyon. Studies by SHEPARD (1951) and LUDWICK (1950) in the San Diego area have shown that displacement of sediment from shallow to deep water appears to be funnelled down the canyons in that area, and it seems probable that much displaced sediment flows down the channels of submarine canyons in other areas of the world. The restriction of displaced sediment to the Mississippi Canyon floor in the present cores is evidence in this connection.

The lower section of core 15, below approximately 165 cm, contains abundant sand grains and plant fibres; this sediment contains no benthonic Foraminifera which are characteristic of water shoaler than that at which the core was collected (298 m). It is possible that this sediment was displaced from shallow water, but the absence of displaced Foraminifera suggests that a turbidity current was not the mechanism of deposition. It appears more likely that this material may be river sediment which was carried offshore (approximately 20 miles) during flood stages of the Mississippi River. Shallow-water Foraminifera would not be expected under these conditions.

It is suggested that the occasional specimens of shallow-water Foraminifera found in cores 3–8 and 13–14 do not indicate the presence of appreciable amounts of displaced sediment in these cores. These specimens may have been deposited by one or more of the following mechanisms:

(1) They may have been carried somewhat beyond the limit of turbidity flows because of slow settling velocity or low effective specific gravity. If the specimens contained protoplasm this mechanism would be aided.

(2) They may have been put in suspension by wave action when they contained protoplasm, and were carried to their present positions by currents. A few specimens of living, shallow-water benthonic Foraminifera have been reported in offshore plankton tows in the northwestern Gulf of Mexico (PHLEGER, 1951, p. 36).

(3) They may have been deposited by several very small-scale turbidity currents which transported small amounts of sedimentary materials.

The presence of specimens of *Gümbelina* in core 10 is difficult to explain. These may have been carried out by the river and deposited at their present position, or they may possibly be contaminated by a salt plug bringing early Tertiary or Cretaceous sediments to the surface.

REFERENCES

FUGLISTER, F. C. (1947), Average monthly sea surface temperatures of the western North Atlantic Ocean. *Papers in Phys. Oceanogr. and Meteorol., Mass. Inst. Tech. and Woods Hole Oceanogr. Inst.*, **10** (2), 5–25.

GEALY, B. L. (1955), Topography of the continental slope in northwest Gulf of Mexico. *Bull. Geol. Soc. Amer.*, **66**, 203–228.

HVORSLEV, M. J. and STETSON, H. C. (1946), Free-fall coring tube: a new type of gravity bottom sampler. *Bull. Geol. Soc. Amer.*, **57**, 935–950.

LUDWICK, J. C. (1950), Deep water sand layers off San Diego. *Univ. of Calif. at Los Angeles, Doctor's Thesis.*

PARKER, F. L. (1954), Distribution of the Foraminifera in the northeastern Gulf of Mexico. *Bull. Mus. Comp. Zool.*, **111** (10), 453–588.

PARR, A. E. (1935), Report on the hydrographic observations in the Gulf of Mexico and the adjacent straits made during the Yale Oceanographic Expedition on the *Mabel Taylor* in 1932. *Bull. Bingham Oceanogr. Coll.*, **5**, 1–88.

PHLEGER, F. B (1951), Ecology of Foraminifera, northwest Gulf of Mexico. Part I, Foraminifera distribution. *Mem., Geol. Soc. Amer.*, **46**, 1–88.

PHLEGER, F. B (1954), Foraminifera and deep-sea research. *Deep-Sea Research*, **2**, 1–23.

PHLEGER, F. B and PARKER, F. L. (1951), Ecology of Foraminifera, northwest Gulf of Mexico. Part II, Foraminifera species. *Mem., Geol. Soc. Amer.*, **46**, 1–64.

PHLEGER, F. B, PARKER, F. L. and PEIRSON, J. F. (1953), Sediment cores from the North Atlantic Ocean. No. 1, North Atlantic Foraminifera. *Repts. Swedish Deep-Sea Exped.*, 7, 3–122.

SHEPARD, F. P. (1951), Sand and gravel in deep-water deposits. *World Oil*, 61–68.

STETSON, H. C. (1953), The sediments of the western Gulf of Mexico. Part I, The continental terrace of the western Gulf of Mexico: its surface sediments, origin and development. *Papers in Phys. Oceanogr. and Meteorol.*, 12 (4), 1–45.

TRASK, P. D. (1953), The sediments of the western Gulf of Mexico. Part II, Chemical studies of sediments of the western Gulf of Mexico. *Papers in Phys. Oceanog and Metrorol.*, 12 (4), 49–120

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 58-67.

Seasonal changes in the phytoplankton as indicated by spectrophotometric chlorophyll estimations 1952-53

By PAMELA G. JENKINS

(Introduction by W. R. G. ATKINS)

Summary—Estimations of the chlorophyll content of the phytoplankton in the English Channel at station E1 were continued from September 1952 until August 1953 at ten depths from 0 to 70 m. As before, the species of the phytoplankton were identified by a culture method.

Minima of about 2 mg/m^3 occur in winter and in June. Maxima at particular depths can occur in March, April or May, thus in 1952 the maximum was in a March surface sample, 34·2 mg m^3, whereas in 1953 sinking of the cells gave, in May, 78·8 mg m^3. The quantity found can be much influenced by the date of sampling. An autumn maximum late in September 1952 gave 21·1 mg m^3 at the surface.

The collodion filter disks varied in colour from dark grey or chocolate to a light sandy colour and examination with a low-power microscope shows phytoplankton, stray fibres and sometimes copepods and other animals. Copepods were counted in spring and summer, a maximum of 24 on one disk being found at 25 m on April 27, got from two litres of water. The figures for the column indicate about 300,000 per square metre down to 70 m.

The botanical composition of the phytoplankton was studied by the repeated examination, from first signs of growth onwards, of the chemically enriched samples placed in diffuse daylight. Fifty-four species of Bacillariphyceae were recorded. As before *Skeletonema costatum*, a *Navicula sp.* and *Nitzschia closterium* were the most common. Many species of *Chaetoceros* were identified in the autumn of 1952.

Six species of the Chlorophyceae, five of the Chrysophyceae, one of the Cyanophyceae and three of the Cryptophyceae were recorded. The most common species of the first class was a *Chlorella*, and of the second a species of *Coccolithophora* grew in each sample. *Phaeocystis globosa* grew from January to May. The member of the Cyanophyceae was an *Oscillatoria*. Neither this nor *Phaeocystis* was recorded for E1 in the previous year. *Hemiselmis rufescens* appeared once more.

INTRODUCTION

IN THIS " Festschrift " number it may well be pointed out that the roots of the science of the sea are sunk deep in time. The adequate study of the sea involves all the exact sciences, including even astronomy, and all the biological sciences.

It is not, as often considered, a preserve for zoologists. The early devotees of the study of marine life were just biologists, mainly systematists, for of necessity one must follow Adam and name things. The beautifully illustrated papers of the early workers are highly educational, and remind one that it is not for us to misquote and say, " Surely we are the people and wisdom shall die with us ". I recall with sadness a morning in April 1941 when, in smoking Plymouth, I picked up one page of an old biological work—all that remained of our Athenaeum Library, which had housed so much of the older literature.

Perhaps Dr. BIGELOW may be considered as having begun at about the end of the old era of amateur biologists. He was studying the phytoplankton of the Gulf of Maine in 1913. He found the entire basin occupied by a peridinian plankton, but never found diatoms in abundance in July or August except close along the coast and on Georges Bank.

So when, largely by his efforts, the Woods Hole Oceanographic Institution was founded, they could begin with a basic knowledge of the phytoplankton which is still lacking in Plymouth. But quantitative work on the production of phytoplankton in the English Channel has been carried out since 1921, first by calculation from the changes in hydrogen ion concentration brought about by photosynthesis (1922) and since 1922 from the consumption of phosphate (1923). The arrival of a modern spectrophotometer however made it possible to estimate the phytoplankton crop by extracting the chlorophyll from collodion filter membranes on which even the smallest green flagellates had been retained. This was done in the year 1951–52, and by a culture method, similar to that of bacteriology, the organisms were grown and multiplied so that even those originally very sparsely distributed were not missed (ATKINS and JENKINS, 1953).

The chlorophyll method of course gives the phytoplankton content of the water when sampled, whereas the phosphate calculations give the amount produced over a period. The two may be very different. A beginning was thus made in obtaining a better knowledge of what plants were present—and of when they flourished—also such work provides a basis for the study of the movement of water masses tagged by a known algal flora.

I therefore asked my collaborator Miss P. G. JENKINS to continue this research and to give her results, which she has done as follows.

W. R. G. A.

ORIGIN OF SAMPLES AND THEIR EXAMINATION

Water was collected with a Nansen-Pettersson water bottle at the international hydrographic station England No. 1 (E1), twenty miles S.W. from Plymouth, at a series of depths from 0 m to 70 m bottom. Two litres of each sample were filtered through a collodion (Gradocol) membrane of average pore diameter one micron.

The phytoplankton cells and the suspended matter which remained on the disks were examined under the low-power microscope. Then 10 ml of an 80 per cent aqueous acetone solution was used to extract the plant pigments from each membrane.

A " Unicam " spectrophotometer with 4·0 cm cuvettes served to measure the minimum percentage transmission in the red between 640 and 670 mμ. These values were converted into concentrations of chlorophyll in mg/l read off from a graph of the transmissions of 80% aqueous acetone solutions of a dry commercial chlorophyll plotted against their concentrations. This graph and the absorption spectrum of the chlorophyll may be seen in the 1953 paper. Using 10 ml of the aqueous acetone to extract the plankton from a litre of water, it is obvious that the chlorophyll has been concentrated one hundred times, so 1 mg/l as read off is equivalent to 0·01 mg/l or to 10 mg/m^3. An allowance was of course made for the actual volume extracted.

In winter, i.e. November to February, the colour of the extracts was slightly yellow and the green was almost imperceptible. The colour deepened with the spring growth to a deep olive green, and lightened in the summer samples.

EXAMINATION OF THE PLANKTON ON THE DISKS

The disks varied in their intensity from a dark grey or chocolate to a very light sandy colour. It was impossible to deduce the amount of chlorophyll in the extracts from these shades. That deduction could only be made when the disks were a uniform faint green. They were often covered with diatoms of various species, and at times had green spots due to the presence of some species of the Chlorophyceae. The Dinoflagellate *Ceratium tripos* occurred at every depth on Aug. 10, 1953. Fibres were frequently seen. Many copepods were found on the disks and as they were so numerous in the spring of 1953, their numbers were counted and set out in Table I. The totals in the second line from the bottom (Σ means) are based on the sum of the means for 2·5, 7·5, 12·5, . . . 67·5 m for 14 depths. This sum is then multiplied by 5 (for 5 m intervals) and the totals in the bottom line are expressed as the number of copepods in the column per square metre of surface, namely in 70 m^3. (The amounts of chlorophyll in the water column (Fig. 5) to be considered later were conducted in the same way.)

These totals were included because the phytoplankton and zooplankton crops are obviously related. In 1951–52 some medusae were found but none could be seen in the following year. Nudibranch veligers were found from June to August, though not previously seen on the disks.

Table I—Numbers of Copepods found on collodion membrances from April until August 1953, in 2 litres of water at station E1

Depth (*m*)	*April* 13*th*	*April* 27*th*	*May* 11*th*	*June* 22*nd*	*July* 20*th*	*August* 10*th*
0	0	4	16	4	11	0
5	4	6	14	5	4	0
10	—	—	—	—	—	3
15	3	10	22	6	15	2
20	10	7	14	7	15	9
25	7	24	3	12	18	8
30	10	6	10	1	14	6
40	6	9	5	—	12	0
50	3	7	4	6	4	3
70	5	9	14	0	3	0
Σ means*	70	124	148	62	130	45
thousands per m^2 in column	175	310	370	155	325	112

* See text, p. 59.

Table II—Diatoms identified in enriched cultures exposed to light

Signs: — Not found A present B more frequent
C plentiful D very plentiful O not found in one of the two cruises

Where two letters occur for one month, two cruises were undertaken

BACILLARIOPHYCEAE	*Years*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
COSCINODISCACEAE													
Coscinodiscus sp.	1952	—	—	B	—	—	—	—	—	A	A	—	B
	1953	C	—	—	—	—	—	—	—	—	—	—	—
C. concinnus	1952	—	—	—	—	—	—	—	—	—	A	—	—
C. excentricus	1952	—	—	—	—	—	—	—	—	C	—	—	—
C. radiatus	1952	—	—	—	—	—	—	—	—	A	—	—	—
Melosira moniliformis	1952	—	—	B	D	C	B	—	A	B	—	—	—
	1953	A	—	CO	AO	—	—	—	—	—	—	—	—
Paralia sulcata	1952	—	B	—	—	—	—	—	—	—	A	—	—
	1953	—	—	AO	AO	—	—	—	—	—	D	—	—
Skeletonema costatum	1952	—	—	B	—	A	—	B	C	D	D	B	B
	1953	—	—	DO	BO	—	OB	A	B	D	D	D	D
Thalassiosira sp.	1952	—	—	—	—	—	—	—	—	—	B	—	—
	1953	—	B	BO	—	—	—	A	A	—	—	—	—
T. condensata	1953	—	—	BO	—	—	—	—	—	—	—	—	—
T. decipiens	1952	—	—	—	—	—	—	—	—	B	—	—	—
	1953	—	—	—	—	—	—	—	—	—	DD	D	D
T. gravida	1952	B	—	C	B	—	—	—	—	D	C	D	D
	1953	D	—	BO	—	—	—	—	—	—	—	—	—
T. nordenskioldii	1953	—	—	—	DO	—	—	—	—	—	—	—	D
T. subtilis	1952	—	—	—	—	—	—	—	—	C	—	—	—
	1953	—	—	AO	AO	—	—	—	—	—	DD	D	D
BIDDULPHIACEAE													
Biddulphia sp.	1952	—	—	—	—	—	—	—	—	—	—	A	—
B. regia	1952	—	—	—	—	—	—	—	—	A	—	—	—
B. sinensis	1952	—	—	—	—	—	—	—	—	—	—	A	—
Ditylum brightwellii	1952	—	—	—	—	—	—	—	—	B	D	C	A
	1953	A	—	—	—	—	—	—	—	—	OD	—	—
Eucampia zoodiacus	1953	A	—	—	—	—	—	—	—	—	—	—	—

(*Table II cont.*)

BACILLARIOPHYCEAE	*Years*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
CHAETOCERACEAE													
Chaetoceros sp.	1952	B	—	—	—	—	—	—	D	C	—	A	C
	1953	A	A	BO	—	—	OB	B	C	D	OD	—	—
C. affine	1952	—	—	—	—	—	—	—	—	A	—	—	—
	1953	—	—	—	—	—	—	A	—	—	—	—	—
C. ceratosporum	1952	—	—	—	—	—	—	—	—	A	A	A	—
	1953	A	—	—	—	—	—	—	D	—	—	—	—
C. compressum	1952	—	—	—	—	—	—	—	—	A	—	—	—
C. convexicorne	1952	—	—	—	—	—	—	—	—	A	—	—	—
	1953	—	—	—	—	—	—	B	—	—	—	—	—
C. convolutum	1952	—	—	—	—	—	—	—	—	A	—	—	—
C. curvisetum	1953	—	—	—	—	—	—	B	—	—	—	—	—
C. danicum	1952	—	—	—	—	—	—	—	—	A	—	—	A
	1953	—	—	—	—	—	OA	—	—	—	—	—	D
C. debile	1952	—	—	—	—	—	—	—	—	C	D	C	B
	1953	A	—	—	—	—	—	—	—	—	—	—	—
C. decipiens	1952	—	—	—	—	—	—	—	—	A	A	A	—
	1953	—	—	AO	—	—	OA	—	—	—	OD	D	—
C. densum	1952	—	—	—	—	—	—	—	—	A	—	—	—
C. didymum	1952	—	—	—	—	—	—	—	—	—	A	D	—
	1953	B	—	—	—	—	—	—	—	—	—	—	—
C. gracile	1952	—	—	—	—	—	—	—	—	B	—	—	—
C. laciniosum	1953	—	—	—	—	—	—	A	—	—	—	—	—
C. lorenzianum	1953	—	—	—	—	—	—	A	—	—	—	—	—
C. pseudocrinitum	1952	—	—	—	—	—	—	—	—	—	A	—	A
	1953	—	—	—	—	—	—	—	A	—	—	—	—
C. scolopendra	1952	—	—	—	—	—	—	—	—	A	A	—	—
C. septentrionale	1952	—	—	—	—	—	—	—	—	A	—	—	—
C. simplex	1952	—	—	—	—	—	—	—	—	A	—	—	—
	1953	A	—	—	DO	—	—	A	—	—	—	—	—
C. sociale	1952	—	—	—	—	—	—	—	—	A	—	—	—
	1953	—	—	AO	—	—	—	—	—	—	—	—	—
C. teres	1952	—	—	—	—	—	—	—	—	—	—	B	—
LEPTOCYLINDRACEAE													
Lauderia borealis	1952	—	—	—	—	—	—	—	—	—	—	—	B
	1953	C	—	DO	BO	—	—	—	A	—	—	—	—
Leptocylindricus danicus	1952	—	—	—	—	—	—	C	B	A	A	—	—
	1953	—	—	—	—	—	—	—	C	D	DD	—	—
RHIZOSOLENIACEAE													
Rhizosolenia sp.	1953	B	—	—	—	C	—	—	—	—	—	—	—
R. alata var. *indica*	1952	—	—	—	—	—	—	A	C	A	A	—	—
	1953	—	—	—	—	—	OB	D	D	—	—	—	—
R. fragilissima	1952	—	—	—	—	—	—	—	—	—	A	—	-
R. hebetata	1952	—	—	—	—	—	—	—	B	—	—	—	—
	1953	—	—	—	—	—	—	A	—	D	DD	—	—
R. setigera	1953	—	—	—	—	—	OA	—	—	—	—	D	D
R. shrubsolei	1952	—	—	—	—	—	—	—	—	A	A	—	—
	1953	—	—	OA	—	—	OD	D	—	—	—	—	—
R. styliformis	1953	—	—	—	—	—	—	A	—	—	—	—	—
FRAGILARIACEAE													
Asterionella japonica	1952	—	—	B	—	B	—	—	B	C	D	—	—
	1953	—	—	—	—	—	—	—	—	—	DD	D	—
Fragilaria sp.	1952	—	—	—	B	A	—	A	—	C	D	—	—
F. oceanica	1953	A	—	DA	AO	—	OD	—	A	A	—	—	—
	1952	—	—	—	—	—	—	—	B	B	—	—	—
F. striatula	1953	—	—	—	AO	—	—	—	—	—	—	—	—
TABELLARIACEAE													
Thalassionema nitzschioides	1952	—	—	—	—	—	—	—	A	D	C	D	—
	1953	A	—	BO	—	—	—		—	D	OD	D	D

(*Table II cont.*)

BACILLARIOPHYCEAE	*Years*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
NAVICULACEAE													
Navicula sp.	1952	—	B	C	D	D	D	C	B	C	D	D	B
	1953	A	A	AA	AB	C	DC	—	A	C	DD	—	—
N. membranacea	1952	—	—	—	—	—	—	—	—	—	A	—	—
N. vanhoffeni	1952	—	—	—	—	—	—	—	—	—	B	—	—
	1953	A	—	DD	AO	—	OA	C	—	—	—	D	—
Pleurosigma sp.	1952	—	—	—	—	—	—	—	—	A	C	D	—
	1953	B	A	AO	—	—	—	—	—	—	—	—	D
BACILLARIACEAE													
Bacillaria paxillifer	1952	—	—	—	—	—	—	—	—	B	—	—	—
Nitzschia closterium	1952	D	C	C	D	A	C	D	C	B	D	D	D
	1953	D	D	DB	DD	D	—	C	D	D	DD	D	D
N. delicatissima	1952	—	—	—	—	—	—	—	D	C	A	D	B
	1953	D	—	—	DB	B	AO	D	D	—	—	—	—
N. seriata	1952	—	—	—	—	—	—	—	B	D	D	—	A
	1953	—	—	—	AO	—	—	—	—	D	DD	D	D

SEASONAL VARIATIONS IN CHLOROPHYLL AND THEIR CONVERSION INTO WET WEIGHT OF PHYTOPLANKTON

Water samples were taken at intermediate depths from the surface down to 50 m from August to October 1952, then down to 70 m from November 1952 to August 1953.

It was decided to extend sampling down to the lowest depth possible, 70 m to give a more accurate survey at E1, so that the chlorophyll content for 70 m was known and

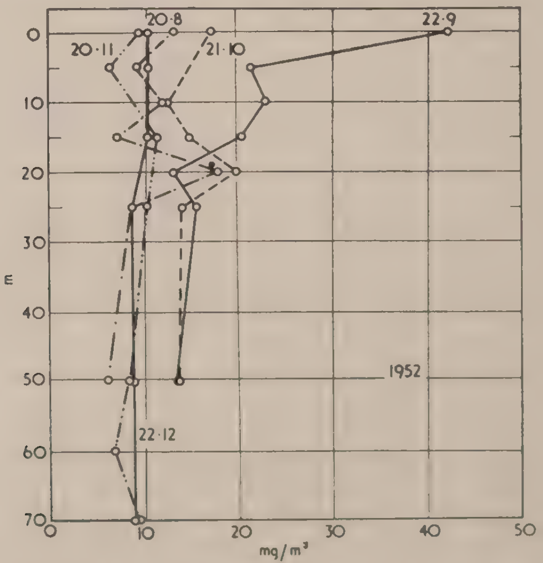

Fig. 1. Variation in chlorophyll from August–December 1952, at Station E1. Ordinates show depth of sampling in metres. Abscissae show concentration of chlorophyll in milligrams per cubic metre.

need not be assumed to be the same as at 50 m, which was done in the 1953 paper. Fig. 1 illustrates the autumn growth from August 1952 (linking up with ATKINS and JENKINS, 1953, Fig. 7) to October, with a surface outburst in September. Growth fell to a value almost uniform with depth during November and December in an almost isothermal water column.

Table III—Algae identified in enriched cultures exposed to light

Signs: — not found
A present
B more frequent
C plentiful
D very plentiful
O not found in one of the two cruises

Where two letters occur for one month, two cruises were undertaken

CHLOROPHYCEAE	*Years*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
CHLAMYDO-MONADACEAE													
Chlamydomonas sp.	1952	—	—	B	—	—	—	—	—	C	D	D	A
	1953	C	C	BB	OA	—	DA	—	—	B	—	A	—
POLYBLEPHARIDACEAE													
Pyramimonas sp.	1952			C	—	B	—	—	—	—	—	—	B
	1953	—	A	—	OC	—	—	A	—	-	—	—	—
CHLORELLACEAE													
Chlorella sp.	1952	—	—	D	D	D	C	B	A	A	D	C	D
	1953	D	B	BB	—	A	DB	—	—	—	—	—	—
ULOTRICHACEAE													
Stichococcus sp.	1952	—	—	C	D	C	C	B	—	—	—	—	—
	1953	—	—	OB	OA	—	DO	—	—	—	—	D	—
Ulothrix subflaccida	1952	—	A	—	—	—	—	—	—	—	—	—	—
	1953	—	A	AO	AO	—	—	—	—	—	—	—	—
CHAETOPHORACEAE													
Ectochaete sp.	1952	—	—	C	D	A	C	—	—	B	A	A	A
	1953	A	—	AO	—	—	OC	—	—	—	—	—	—
CHRYSOPHYCEAE													
Chrysomonad sp.	1952	—	—	—	—	—	—	B	—	—	—	—	—
	1953	B	C	—	—	—	—	—	—	—	—	—	B
Coccolithophora sp.	1952							D	D	D	D	D	D
	1953	D	D	CD	DC	D	DD	B	D	D	DD	D	D
ISOCHRYSIDACEAE													
Dicrateria sp.	1953	—	—	—	OC	—	BC	—	—	—	—	—	—
OCHROMONADACEAE													
Ochromonas sp.	1953	A	A	—	—	—	—	—	—	—	—	—	—
CHRYSOCAPSACEAE													
Phaeocystis globosa	1953	A	A	OC	DB	D	—	—	—	—	—	—	-
CYANOPHYCEAE OSCILLATORIACEAE													
Oscillatoria sp.	1953	A	—	—	OA	—	—	—	—	—	—	—	—
CRYPTOPHYCEAE													
Cryptomonad sp.	1952	—	—	—	—	—	—	B	—	—	—	—	B
	1953	—	—	—	BA	—	—	—	—	—	BB	A	A
Cryptomonas sp.	1952	—	—	—	—	—	—	—	—	—	—	A	—
	1953	B	C	-	—	—	—	—	—	—	—	—	—
Hemiselmis rufescens	1952	D	—	—	—	—	—	—	—	—	—	D	D
	1953	—	—	—	OC	—	—	—	—	B	OD	—	—

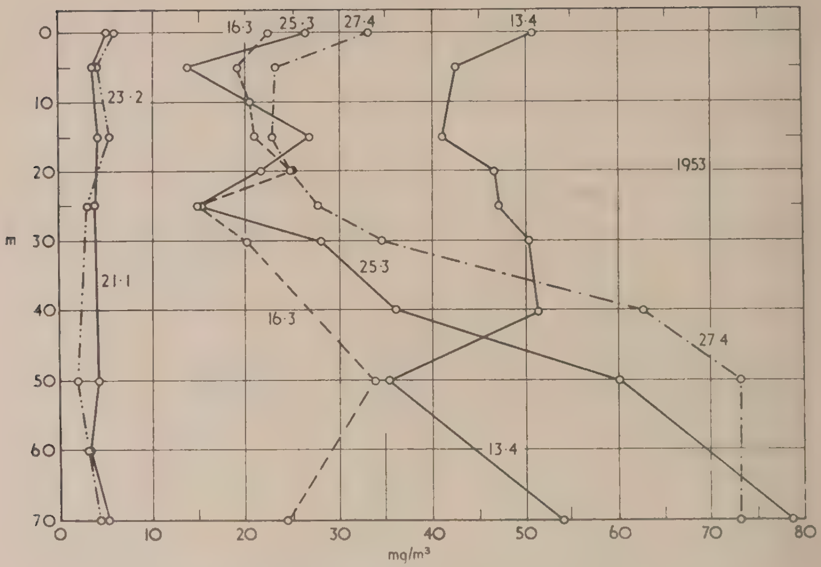

Fig. 2. Variation in chlorophyll, January–April 1953 at E1, in mg/m³.

The two winter months showed no appreciable change (Fig. 2), but from March onwards the samples gave a high value of chlorophyll at the surface and even at 70 m, giving a bottom maximum at 70 m of 78·8 mg/m³ on March 25th. These high readings for the lower depths showed that the cells must have sunk. RILEY (1941 B) observed this high concentration of chlorophyll from 40–70 m at Georges Bank during March and April. MARSHALL and ORR long ago (1928) reported that " during the spring

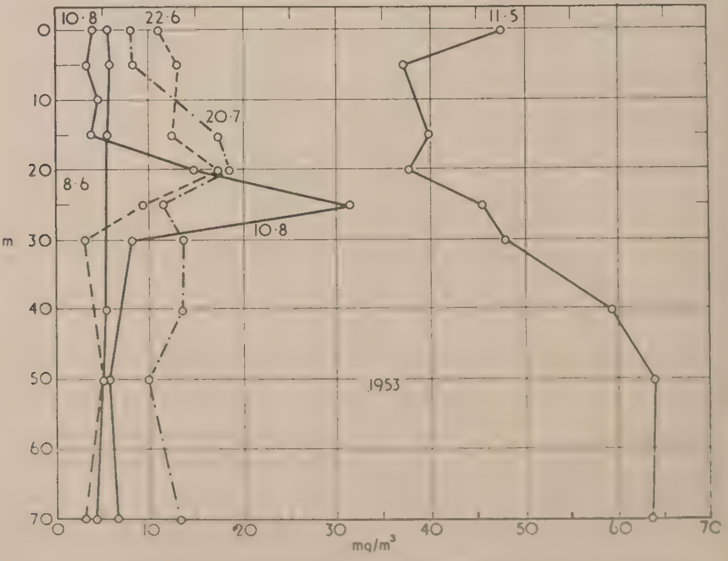

Fig. 3. Variation in chlorophyll, May to August 1953 at E1, in mg m³.

months it was not uncommon in shallow water to find more plankton near the bottom than anywhere else ". They also found that during the spring outburst the phytoplankton caused such a great reduction in submarine illumination that the compensation point (or depth) was at times raised to 5 m or less.

The sudden drop from spring growth, May 11th to the summer minimum, June 8th, is seen in Fig. 3. The May readings were very high due to the abundance of *Phaeocystis globosa*. Two filtrations were necessary because the disks became clogged, so ordinary filter paper was first used and then the special membrane. Each of these was extracted twice. The later cruises show the gradual growth near the thermocline, building up to the autumn maximum, with a peculiar outburst at 25 m on August 10th of 31·5 mg/m^3. This outburst must have occurred in a region where light intensity allows photosynthesis to take place and its occurrence at only this depth is probably due to the absence of sufficient nutrient salts in the upper 15 m.

The results for surface and bottom chlorophyll throughout the year are seen in Fig. 4 with a surface maximum in September and April and a bottom maximum in

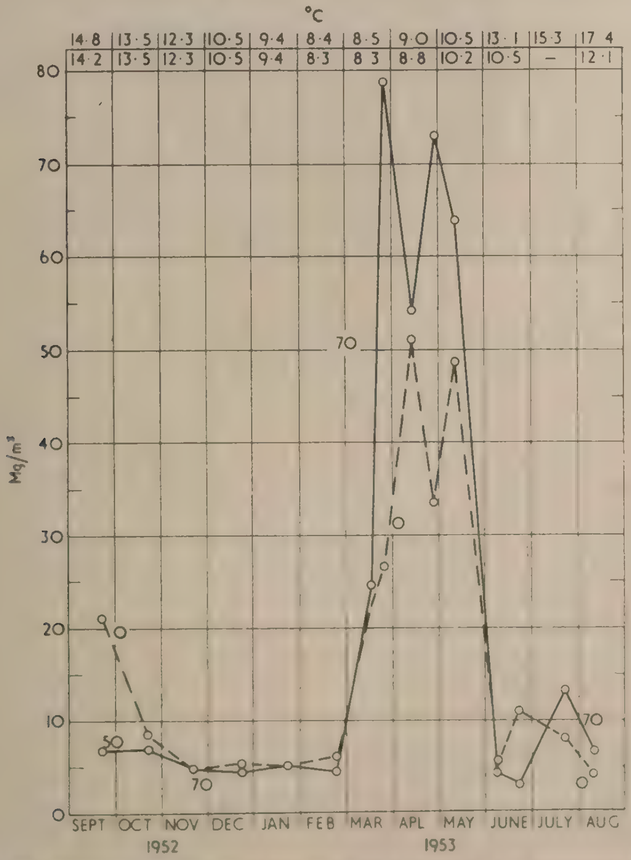

Fig. 4. Surface and bottom concentrations of chlorophyll for 1952–53. The September and November values of 1952 are for 50 m. The ordinates show concentration of chlorophyll at surface and bottom in mg/m^3. The sea temperatures are for the surface, above, and for the bottom (70 m) just below the top line of the frame.

March, due to sinking. The thermoclines for the year were found on September 22nd, 1952, 15 m, 14·6° C; April 27th, 1953, 15 m, 12·5° C; June 22nd, 20 m, 13·0° C; August 10th, 15 m, 17·2° C.

In both 1951 and 1952 the autumn maximum (Fig. 5) was in September, the amounts being respectively 0·59 and 1·02 g m². The spring minimum was in November 1951, but was three months later the following winter when it was reached in February 1953. But the values were identical, 0·25 g m². The spring maximum in April 1952 was 1·33 g/m², but this value was obtained on the assumption that the amount of chlorophyll was uniform beyond the last depth examined, 50 m to 70 m, bottom. Later work showed that, on account of sinking of the cells, this was probably an underestimate. The maximum was in May in 1953, 3·68 g/m² (very much higher) with much Phaeocystis present. Both the summer minima fell in June, 0·15 g m² for 1952 and 0·35 g/m² for 1953.

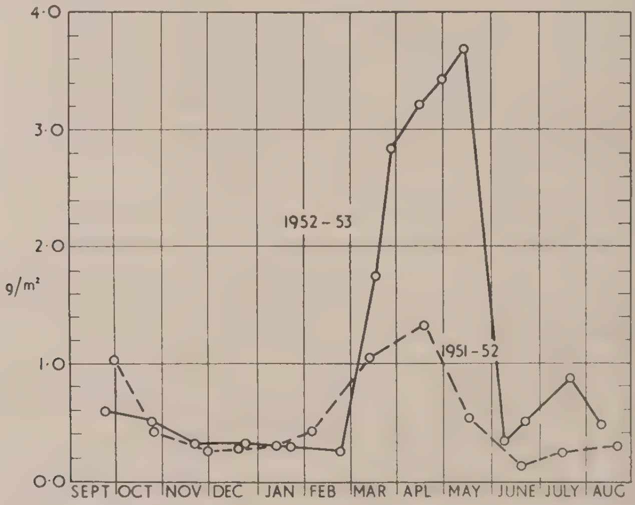

Fig. 5. Variation of chlorophyll in water column, 0–70 m, in grams per square metre for 1951–52 (broken line) and 1952–53 (full line). See text, p. 66.

These chlorophyll quantities may be converted into wet weights of phytoplankton as in the paper of 1953. Taking RILEY's value 2·9% of chlorophyll (1941 A), calculated on the dry weight, and taking the dry weight as 20% of the wet weight, we arrive at a factor 172 by which one can multiply the weight of chlorophyll to convert it to wet weights of phytoplankton. It is recognized that these factors are somewhat arbitrary.

THE BOTANICAL COMPOSITION OF THE PHYTOPLANKTON AT STATION E1

Samples of water, 100 ml, from each depth were poured into conical flasks and enriched with Miquel's solution, 0·2 cc of solution A and 0·1 cc of solution B.

They were placed in a south window during winter and from spring to autumn were illuminated by a diffuse north light. The enrichment of the culture solution gave a better chance for species originally very sparsely represented to multiply and be detected. This amounts, in fact, to the common bacteriological technique.

Tables II and III are an attempt to indicate the relative amounts found in the earlier stages of the cultures, the comparison being between the same species, so different growth rates are not involved.

Table II shows the Bacillariphyceae, identified as named and classified in Hendey's list (1954). Fifty-four species were found, as compared with twenty species found in 1951–52, but the autumn growths cannot be compared with 1951–52 since the samples were not enriched and exposed until February 1952.

Skeletonema costatum, *Navicula sp.*, and *Nitzschia closterium* were again the most regular in occurrence. Species absent from our lists before 1953 were *Thalassiosira condensata* found in February, *Eucampia zoodiacus* in January, *Rhizosolenia setigera* in June, November and December, *R. styliformis* in July, also *Fragilaria striatula* in April.

The Algae listed in Table III are as named and classified in Parke's list (1953). The most regular occurrence of the Chlorophyceae were the *Chlorella sp.* and *Chlamydomonas sp.* The three others listed grew well in the spring, *Ulothrix subflaccida* which was found once in February, 1952, was present from February to early April in 1953.

Of the Chrysophyceae, the *Coccolithophora sp.* were always in the cultures. *Phaeocystis globosa*, which was absent from the 1952 cultures, grew in 1953, increasing to a great mass in May. This caused the blocking of the sea water filtration.

One member of the Cyanophyceae was present in January and late April in 1953, an *Oscillatoria sp.* The growth of such sessile forms as this and the *Ectochaete sp.*, *Ulothrix subflaccida*, and *Stichococcus sp.*, though not truly planktonic showed that some must have been present in the water at the time of sampling.

Hemiselmis rufescens, a species of the Cryptophyceae, which grew in January 1952, was very plentiful in November and December 1952, also in April and the early autumn of 1953.

I would like to express my thanks to Dr. M. V. Lebour, Dr. M. Parke, Dr. T. J. Hart and Mr. T. R. Tozer for much help in the identifications, also Mr. F. A. J. Armstrong for the temperature observations. Finally for the collection of the sea water I have pleasure in thanking the captains and the crews of the R.V. *Sula* and the R.V. *Sarsia*.

REFERENCES

Atkins, W. R. G. (1922), The hydrogen ion concentration of sea water in its biological relations. *J. Mar. Biol. Assoc.*, **12,** 717–771.

Atkins, W. R. G. (1923), The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. *J. Mar. Biol. Assoc.*, **13,** 119–150.

Atkins, W. R. G. and Jenkins, Pamela G. (1953), Seasonal changes in the phytoplankton during the year 1951–52 as indicated by spectrophotometric chlorophyll determinations. *J. Mar. Biol. Assoc.*, **31,** 495–508.

Bigelow, Henry B. (1915), Exploration of the Coast Water between Nova Scotia and Chesapeake Bay, July and August, 1913, by the U.S. Fisheries schooner *Grampus*. Oceanography and Plankton. *Bull. Mus. Comp. Zool.*, **59** (4), 151–359.

Bigelow, Henry B. (1926), Plankton of the Offshore Waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), Document No. 968, 1–509.

Hendey, N. Ingram (1954), A preliminary check-list of British marine diatoms. *J. Mar. Biol. Assoc.*, **33,** 537–559.

Marshall, S. M. and Orr, A. P. (1928), The photosynthesis of diatom cultures in the sea. *J. Mar Biol. Assoc.*, **15,** 321–60.

Parke, Mary W. (1953), A preliminary check list of British marine algae. *J. Mar. Biol. Assoc.*, **32,** 497–520.

Riley, G. A. (1941 a), Plankton studies 3. Long Island Sound. *Bull. Bingham Oceanogr. Coll.*, 7 (3), 1–93.

Riley, G. A. (1941 b), Plankton studies 4. Georges Bank. *Bull. Bingham Oceanogr. Coll.*, 7 (4), 1–73.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 68-73.

Water replacements and their significance to a fishery

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Summary—Attention has been directed to some of the major and more apparent effects that water replacements may have on various fisheries. It has been indicated that such interchanges may be responsible for the destruction of a fish population or the extension of others. The loss of larvae to scallop and haddock areas has been considered as the result of movements of a water mass, and it is suggested that the availability and catchability of certain species is effected by certain water replacement phenomena. When consideration is given to the cycle of life in the sea, it will be quite evident that many indirect effects may follow from these water replacements. While the processes of long-term replacements are not too well understood, wind action is one of the more apparent major casual factors in short-term replacements.

INTRODUCTION

WHILE THE changing characteristics of a water mass, such as temperature and salinity, are followed in detail in the study of a fishery, the replacement of one body of water by another is a process which, generally, only attracts attention when the characteristics of the water bodies concerned are in considerable contrast.

Whether it be of the estuary, a coastal area, or the open ocean, the particles of a water mass are never at rest, being subjected to the internal and external forces of gravity, pressure, wind, tide and the Coriolis force. The resultant movements of the water particles under these forces bring about the flushing of estuaries, the replacement of water masses in a bay or coastal area, the removal of water masses from a fishing bank, and the transportation of large masses of ocean water from one location to another.

The flushing of estuaries has been given considerable attention during recent years, due to the need of considering the many problems of pollution. The principles derived from such studies furnish an insight into the mechanism involved in the replacement of waters in a comparatively small area, almost completely land-bound. In contrast, and on an ocean-wide scale, COOPER (1954, 127), has called attention to the large variations in the phosphate content and biological productivity of the English Channel in the last thirty years. He seeks an explanation in the replacement processes involving the replenishing of deep Atlantic water by potentially rich northern waters, these deep Atlantic waters eventually upwelling to determine the nutrient supply of the coastal waters of north-eastern Europe.

Attention is directed herein to many of the direct consequences to a fishery of the various processes of replacement.

THE DESTRUCTION OF A FISHERY

BIGELOW and WELSH (1925) describe the disaster to the tilefish, which first came to light in March, 1882, when multitudes of dead fish were observed floating on the surface between the latitudes of Nantucket and Delaware Bay on the Atlantic coast. The area of destruction was at least 170 miles long by 25 miles broad, and covered the entire zone inhabited by the tilefish north of Delaware Bay. It is estimated that at least a billion and a half dead tilefish were sighted. There is evidence to indicate that the destruction of this fishery was caused by a sudden temporary flooding of the bottom by abnormally cold water. It has been shown that the tilefish of the Atlantic coast occupies a very definite environment, for it lives only along the upper part of the continental slope where the water temperatures are approximately 10° C, and never ventures into the lower temperatures on the shoaling bottom nearer land. We have in Bigelow and Welsh's account of the disaster to the tilefish, a well-documented record of the significance of a temporary incursion of waters of contrasting temperature, which in this case brought disaster to a fishery.

On the basis of present knowledge, the source of the abnormally cold water responsible for such a flooding is to be found to the eastward. A study of the slope water off the Scotian Shelf (McLellan, *et al.*, 1953), has shown that, between the northern boundary of the slope water and the continental slope, there is found in varying quantities a body of cold water, less than 0·0° C off the Grand Banks, and less than 4·0° C east of Sable Island. The quantity of such water, acting as a cushion between the slope water and the continental slope, decreases with westward progression until the slope water generally makes contact with the continental slope to the westward of Emerald Bank. Northerly and southerly migrations of the northern edge of the slope water regime, and westerly progressions and easterly withdrawals of the colder waters along the continental slope, provide the mechanism for producing sharp and sudden changes in the water temperatures on the continental slope and over the outer areas of the continental shelf. While the disaster to the tilefish was of major import, and the westerly progression of cold water must have been greater than normal, similar phenomena on a less spectacular scale have been noted in recent years.

THE EXPANSION OF A FISHERY

In contrast, both as to time and extent, to the temporary incursion of colder waters, bringing about the destruction of a fishery over a limited area, is the historical record of the expansion of the Greenland fishery in recent years with the strengthening of the Atlantic influence in northern latitudes.

Passing over earlier history, about 1820, cod were known to be present in enormous quantities in West Greenland waters, as far north as Disko Bay (Jensen and Hansen, 1931). Thereafter, they were absent for a long period of years. Between 1845 and 1849, cod were again plentiful in the Greenland area and then entirely disappeared. From 1917 there was a marked upward tendency in the fishery. The catch increased from approximately 1,000 tons in 1925 to greater than 12,000 tons by 1945, and this fishery has persisted to the present. In dealing with the state of the West Greenland Current up to 1944, Dunbar (1946) points out that, by 1928, the waters for the west coast of Greenland were considerably warmer than in the preceding period, and that the peak warm year was reached within the period 1930-40. The increasing Atlantic influence however was clearly evident in Latitude 72° N in 1942. A comparison of oceanographic conditions in Hudson Bay and Hudson Strait, as observed in 1930, with those of 1948 (Bailey and Hachey, 1951) has shown that the observed higher temperatures and salinities of 1948 are indicative of the increasing Atlantic influence in northern waters generally. A meteorological study of Sherbog (Dunbar, 1946), has suggested that the warming of the Arctic and sub-Arctic regions from Greenland to Siberia, which has taken place in recent years, is one manifestation of a large scale climatic cycle of a period of about 225 years, which has presumably passed its maximum. It must be stressed here that the expansion of the Greenland cod fishery is associated with the extension of warmer Atlantic waters into more northerly latitudes, although such an extension is probably associated with the climatic cycle.

THE LOSS OF LARVAE

Studies on the replacement of Bay of Fundy waters were initiated some years ago (Hachey, 1934), and it became evident that the main factors involved in the replacement of these waters were land drainage, wind, and tide. Other things being equal, an excess of south-westerly winds favoured the retention of surface waters within the Bay and thus nullified the normal dynamic tendency for surface outflow and renewal of the waters at greater depths. Under such conditions a type of " closed circulation " is set up within the Bay, as opposed to an " open circulation " when surface waters are carried out of the Bay to be replaced by inflowing deeper waters. During the summer months the " closed circulation " favours higher surface water temperatures, and the surface temperatures, as well as the temperature gradient in the upper layer, can be used as an indication of the type of circulation prevailing. Dickie (1955) has made use of the temperature data for the Bay of Fundy to show that successful year classes of scallop are produced in those years when the " closed circulation " prevails. Not only do the warmer surface waters hasten development of the scallop larvae to the setting stage, but the " closed circulation " favours the retention of the larvae within the Bay where they settle and grow on suitable scallop bottom. Under the " open circulation " system, as indicated by lowered surface temperatures, the larvae are carried out of the Bay and are lost to the Bay of Fundy scallop fishery.

The replacement of Bay of Fundy waters is not necessarily a regular progressive process, even when the " open circulation " system prevails. Ketchum and Keen (1953) have worked out various mean flushing times and exchange ratios for various parts of the Bay of Fundy, and they point out that although their conclusions were based upon the distribution of river water, the same exchanges may be expected for any material or organism transported by the water. Ketchum and Keen calculated an average flushing time of 74 days for that part of the Bay of Fundy between Cape Chignecto and a line south of Grand Manan. Bailey (1953) has shown that within the period October 6th, 1952, and November 21st, 1952, the waters of the Bay of Fundy were almost completely replaced, a replacement that only became apparent when it was found that the salinity throughout a section had increased by more than 0·5‰ within the period. It might be emphasized that within this period of forty-six days (or less), practically all free-moving larvae in the surface layers would have been carried out of the Bay of Fundy. So too would all free-swimming forms which were feeding at random. The higher salinities as found on November 21st indicate that the replacement involved the inward movement of waters originating from sub-surface depths, and these waters would necessarily carry into the Bay non-swimming forms, and free swimming forms which were feeding at random.

According to Walford (1938) the survival of the eggs and larvae of the haddock on Georges Bank is dependent on the variations in the current system in this area, these variations being controlled to a large extent by winds (Bigelow, 1927, 857). He suggests that the loss of the eggs and larval population in 1932, which occurred some time after the first week of March, was due to the removal by currents. Similarly

Bigelow (1926, 77) wrote: " at the time of our March and April visits (to the northeastern part of Georges Bank) in 1920, the presence of newly spawned eggs in abundance right out to the 1,000 metre contour proved that a drift out to sea was then taking place from the southern point of the Bank." Walford (1938, 49) states: " there was a very important difference between the circulatory picture in the season of 1932 and that of the corresponding period in 1931. While in 1931 the water movements were such as to permit the bulk of the eggs to remain on the bank and hatch there, in 1932 there were currents carrying eggs off the northern and southern edges into deep water where they were probably lost to Georges Bank." In summary, Walford (1938, 55) points out that a change in the circulatory system on Georges Bank may be disastrous to the haddock brood, and consequently, may be an important cause of fluctuations in abundance.

Carruthers, *et al.* (1951) have directed attention to the variations in brood strength in the North Sea haddock in the light of relevant wind conditions, and the results of these studies have directed considerable effort to the analysis of wind systems as related to other North Sea Fisheries.

AVAILABILITY OF THE FISH

The displacement of surface waters on a grand scale by wind is amply demonstrated by the great ocean currents of the North Atlantic, and the fundamental principles have been thoroughly outlined in the classical work of Ekman (Sverdrup, *et al.*, 1942, 492). Ekman has shown on a theoretical basis that a surface current set up by wind is directed 45° to the right of the wind direction in the northern hemisphere, and this has been shown by observation to be a satisfactory approximation in deep water. In shallow water the deflection of the surface wind current is smaller. A wind blowing parallel to a coast is thus effective in transporting surface waters towards the coast, when the coast is to the right of the wind (*cum sole* from the wind direction) in the northern hemisphere, and away from the coast when the coast is to the left of the wind.

The capture of young herring along the open coasts of the Bay of Fundy and the Gulf of Maine is chiefly dependent upon fixed shore weirs. Huntsman (1934) states: " that the herring are to a considerable extent quite near the surface during the twenty-four hours of the day is not only a matter of direct observation, but a requisite for successful operation of the weirs." Huntsman also states (1934, 96) that " the herring may be treated as a planktonic form ". It then becomes evident that herring in the surface waters, and considered as a planktonic form, will be moved on or off the shore with the varying direction of the wind. This is particularly pertinent on an open coast, such as that of Maine, and the south coast of New Brunswick, where the availability of the herring to the shore-fixed weirs must be determined in part by the varying strength of the prevailing south-west winds during the summer months.

TEMPORARY ADJUSTMENTS IN A FISHERY

Large scale water replacements of a temporary nature sometimes bring about sharp and sudden changes in water temperature, the changes in environment being sufficient to cause a body of fish to either:

(a) move away from a fishing ground, or

(b) cease feeding and thus fail to be attracted to the bait.

The water replacements in the Halifax area associated with the formation and subsequent movement of a tropical cyclone have been described (HACHEY, 1934), and it has been shown that bottom water temperatures in some of the inshore areas increased from 2·0° C to greater than 15·0° C in less than one week. Under these circumstances, in these areas, all fishing for cod and haddock ceases, and does not resume until temperatures return to more normal values (HACHEY, 1934; MCKENZIE, 1934; VLADYKOV, 1933).

Incursions of warmer slope water over the Scotian Shelf have been observed (HACHEY, 1953), when bottom temperatures reached values as high as 12·0° C, about five degrees above normal seasonal temperatures. While no records of fishing effort are available for periods in which such incursions have been observed, it is well known that such bottom water temperatures are unfavourable to cod and haddock, the groundfish probably moving out of the areas subjected to the incursions of waters of such temperatures.

BARREN SEA FLOOR

In the Gulf of St. Lawrence comparatively extreme variations in temperature and salinity have been observed at depth during the summer months (LAUZIER, 1952) brought about by oscillations of the various water layers of contrasting characteristics on a gradually shoaling sea floor. It has been pointed out by LAUZIER that organisms which cannot tolerate these sudden changes in temperature and salinity will not form important populations along the margins of the Magdalen Shallows, and HUNTSMAN (1918) has shown that there are bands of the sea floor between Cape Breton and the Magdalen Shallows which are comparatively barren. The oscillation of these water layers of contrasting temperatures is probably responsible for the periodic complete destruction of scallop beds which become temporarily established and fishable under marginally satisfactory conditions in the Magdalen Shallows (Annual Report for 1953, Fisheries Research Board of Canada, 34).

MARGINAL FISHERIES

In Canadian Atlantic waters, which are contained in the area of confluence of three current systems with waters of contrasting characteristics, extreme contrasts in water characteristics, chiefly temperature, are to be observed. Very sharp boundaries, both vertically and horizontally, are thus encountered, and various marine organisms suitable to one environment (frigid) or another (temperate) exist on a marginal basis. A small vertical or horizontal change in the margin sometimes exerts a very pronounced effect on a fishery.

With progressive warming of the waters during recent years we have witnessed the northerly expansion of successful oyster production in the Gulf of St. Lawrence, and the northerly extension of the green crab to the Bay of Fundy (Annual Report for 1953, Fisheries Research Board of Canada, 25). As mentioned earlier in this paper, the expansion of the west Greenland cod fishery is probably the most outstanding result of the increased Atlantic influence in northern waters. It is to be expected that a downward trend of temperatures would bring about a recession of these extensions.

In some cases, man is responsible for changes in environmental conditions, and this is particularly true in estuaries where pollution problems arise with present-day industrial developments. Of a different nature are the possible changes in the environment of Georges Bay, between Cape Breton and the Nova Scotia mainland, which may follow from the completion of the Canso Causeway. By cutting off the interchange between Gulf waters and those of the open Atlantic through Canso Strait, the strong possibility exists that the waters of Georges Bay will be warmer than heretofore. Slight upward changes in the water temperatures in this area may be sufficient to exert some influence on the lobster populations, and to bring about a southward extension of the oyster populations of neighbouring areas.

REFERENCES

BAILEY, W. B. and HACHEY, H. B. (1951), An increasing Atlantic influence in Hudson Bay. *Proc. Nova Scot. Inst. Sci.*, **22** (4), 17–34.

BAILEY, W. B. (1953), Seasonal variations in the Bay of Fundy. *Fish. Res. Bd., Canada, Manuscript Rept.*, No. 551.

BIGELOW, H. B. (1926), Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 1–509.

BIGELOW, H. B. (1927), Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 511–1027.

BIGELOW, H. B. and WELSH, W. W. (1925), Fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (1), 1–566.

CANADA, FISHERIES RESEARCH BOARD (1953), Annual Report, Ottawa, 185 pp.

CARRUTHERS, J. N., LAWFORD, A. L., VELEY, V. F. C. and PARRISH, B. B. (1951), Variations in brood-strength in the North Sea haddock in the light of relevant wind conditions. *Nature*, **168**, 317–319.

COOPER, L. H. N. (1954), Deep sea oceanography and biological productivity of shallow seas. *Repts. and Abstr. of Communications, Assoc. Océan. Phys., Union Géod. Géophys. Int., General Assembly*, Rome, Sept. 1954, 148 pp.

DICKIE, L. M. (1955), Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd., Canada* (in press).

DUNBAR, M. J. (1946), The state of the West Greenland Current up to 1944. *J. Fish. Res. Bd., Canada*, **6** (7), 460–471.

HACHEY, H. B. (1934), The replacement of Bay of Fundy waters. *J. Biol. Bd., Canada*, **1** (2), 121–131.

HACHEY, H. B. (1934), The weather man and coastal fisheries. *Trans. Amer. Fish. Soc.*, **64**, 382–389.

HACHEY, H. B. (1935), The effect of a storm on an inshore area of markedly stratified waters. *J. Biol. Bd., Canada*, **1** (4).

HACHEY, H. B. (1953), A winter incursion of slope water on the Scotian Shelf. *J. Fish. Res. Bd., Canada*, **10** (3), 148–153.

HUNTSMAN, A. G. (1918), The vertical distribution of certain intertidal animals. *Trans. Roy. Soc., Canada*, Ser. III, **12** (4), 53–60.

HUNTSMAN, A. G. (1934), Herring and water movements. *James Johnstone Memorial Volume*, 81-96, Univ. Press of Liverpool, 348 pp.

JENSEN, A. S. and HANSEN, P. M. (1931), Investigations on the Greenland Cod (*Gadus callarias* L.) with an introduction on the history of the Greenland cod fisheries. *Cons. Perm. Int. Expl. Mer. Rapp. Proc. Verb.*, **52**, 3–41.

KETCHUM, B. K. and KEEN, D. J. (1953), The exchange of fresh and salt waters in the Bay of Fundy and in Passamaquoddy Bay. *J. Fish. Res. Bd., Canada*, **10** (3), 97–124.

LAUZIER, L. (1952), Effect of storms on the water conditions in the Magdalen Shallows. *J. Fish. Res. Bd., Canada*, **8** (5), 332–339.

MCKENZIE, R. A. (1934), Cod and water temperatures. *Fish. Res. Bd., Canada, Atlantic Stas., Prog. Repts.*, No. 12, 3–6.

MCLELLAN, H. J., LAUZIER, L., and BAILEY, W. B. (1953), The slope water off the Scotian Shelf. *J. Fish. Res. Bd., Canada*, **10** (4), 155–176.

SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. H. (1942), *The Oceans*, Prentice-Hall Inc., New York, 1087 pp.

VLADYKOV, V. D. (1933), High temperature stops haddock fishing. *Fish. Res. Bd., Canada, Atlantic Stas., Prog. Repts.*, No. 7, 10–11.

WALFORD, L. A. (1938), The effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglifinis*) on Georges Bank. *Bull. U.S. Bur. Fish.*, **49**, 1–73.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 74-91.

Sir C. Wyville Thomson's correspondence on the "Challenger" fishes

By Daniel and Mary Merriman
Bingham Oceanographic Laboratory, Yale University

HISTORICAL ACCOUNT

Wyville Thomson's correspondence with Albert Günther, Keeper of the Department of Zoology in the British Museum, about the disposition and study of the fishes taken on the H.M.S. *Challenger* expedition, 1872–1876, and about the publication of results, extended from 1877–1881. In a sense this correspondence centred around the year 1879—the year in which Henry Bryant Bigelow was born on October 3rd in Boston, Massachusetts.*

Now-a-days it is common practice to call oceanography a " new " science. The speed with which it has advanced and, accordingly, with which our knowledge of the oceans has increased, is generally recognized. None the less, it is not altogether easy to maintain perspective and to realize that " . . . the famous ' Challenger ' reports, which may be said to form the solid base upon which the superstructure of the science of oceanography has since been built " (Russell and Yonge, 1928), began first to be published only three-quarters of a century ago—in short, during the life-time of the man whom this volume honours. For this reason, it is perhaps worth looking with some care at the year 1879, both in its broad and special aspects, before turning to the hitherto unpublished correspondence which is the subject of this paper.

The second half of the 19th century in Europe was marked by many political and economic changes stemming from the Industrial Revolution. As a result of the Franco-Prussian war (1870–1871) there emerged a united Germany and a unification, too, of the Italian States. Russia had effectively pushed the Turks back into Asia, but the western powers resisted her attempts to obtain Constantinople and a command of the eastern Mediterranean. With the Congress of Berlin in 1878 the independence of the Balkan countries, Montenegro, Servia, and Roumania, was established. And the alliance of Germany and Austria-Hungary in 1879 proved most aggravating to Italy, who feared it would block her potential control of the Adriatic; to France, who saw it as a blow to her ambition to regain Alsace-Lorraine; and to Russia, who still wanted a foothold in the Balkans and the Mediterranean. China posed problems in the Far East, as the western powers and Russia both tried to gain concessions to her great natural resources.

In the United States, 1879 was a singularly happy and prosperous year. Crops flourished, manufacturing and trade were stimulated, and the railroads were expanding to meet these demands. We were at peace with the world, except for Indian skirmishes in the west where Sitting Bull had been forced to retreat across the Canadian border.

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* The October 3rd, 1879, edition of the London *Times* carried an admonition that there were 12 different Bostons in the U.S.A., and that the name of the state on the envelope address would facilitate accurate delivery.

England, it is said, was not so happily situated that year. There were wide crop failures and a continuing depression. Ireland, with the loss of her potatoes due to adverse weather, was agitating for Home Rule and land rent reforms; the situation was so acute that the American Irish were sending $10,000 a week towards relief in the homeland. England was fighting in Afghanistan to protect her affairs in India. She was also engaged in military operations in South Africa to keep this portion of her Empire. And she was even sending warships to the west coast of South America, where Chile and Peru were fighting, in order to guard her " . . . interests in guano for the fields of Yorkshire ". However, England's firm policy of colonization was to stand her in good stead. In addition to India and South Africa, she had acquired control of the Suez Canal, and had long since colonized Australia, New Zealand, Tasmania, and Canada—this, as other countries, notably Spain, had tended to lose their colonial domains. In a different context, Charles Darwin at the age of 70 in 1879,[*] just twenty years after the publication of *The Origin*, was doing the experimental work at Down which led to the publication in 1881 of *The Formation of Vegetable Mould through the Action of Worms*, to be received " . . . with what struck Darwin as 'laughable enthusiasm' " (Moore, 1955). And the " episcophagous " Huxley had turned to more peaceful pursuits and was preparing to publish *The Crayfish* (1880). It was not, after all, such a bad year for England.

Perusal of the London *Times* in the year 1879 yields amusing coincidence with today. The *New York Herald* was sponsoring a naval vessel's exploration of the North Pole.[†] The *Macon* (Georgia) *Telegraph* reported, and got space in the London *Times* on January 1, 1879, that there was a remarkable phenomenon on the Florida coast where " . . . dark, reddish water " was killing fish and creating " . . . a pestilential stench "; the account went on to state, " We have no other explanation of the poisoning " (reported to have extended as far as 150 miles into the Gulf) " than that it comes from inland waters—the everglades predominantly. . . . " Panama had a revolutionary outbreak. The stevedores on the piers of New York were striking. A large underground cave in Algeria was found to contain blind fish.[‡] Even the book titles have a familiar ring: we read reviews of " The Sea, its Stirring Story of Adventure, Peril, and Heroism " by F. Whymper. " The Broad, Broad, Ocean ", " Notable Voyages ", and " Episodes of the Sea " are a few others of the spate. And another Mr. Whymper[**] was bringing out " The Ascent of Matterhorn ".

We are also struck by many changes. In 1879 Woolworth opened his first store in Utica, New York (in 1955 the Woolworth Company reported its sales for the previous year at an all time high of $721,312,990). In 1879 Harvard College offered 112 scholarships varying from $40 to $350—today it offers over 1,000 scholarships at an average worth of nearly $700 each. In 1879 the Shah of Persia was planning to undertake a pilgrimage to Meshhed with 10,000 troops, while this year the Shah's travels have carried him to Sun Valley and Florida. In 1955 the production of synthetic diamonds has been achieved, finally bearing out the statement in 1879 by NEVIL STORY MASKELYNE of the Mineral Department of the British Museum, " . . . that (this problem) will be solved, no scientific mind can doubt ". In Boston on December 3, 1879, the *Atlantic Monthly* gave a party for the seventieth birthday of the " Autocrat of the Breakfast Table "; today it would be hard to rival the distinction of the gathering which included beside O. W. HOLMES these others: H. B. STOWE, J. G. WHITTIER, H. W. LONGFELLOW, R. W. EMERSON, MARK TWAIN, W. D. HOWELLS, and J. W. HOWE. The February 11th issue of the 1879 London *Times* carried the statement that, " Arrangements are being settled with the Société Générale d'Electricité for an experimental lighting of the reading-room of the Museum with the electric light ". And the April 10th issue reported that communication by telephone was established between the Royal Institution and Burlington House, " . . . with Professor TYNDALL at one extremity of the wire and Professor HUXLEY at the other "; there was apparently much amusement among those present, and, " The feasibility of telephonic communication was clearly demonstrated, the voice being distinctly audible over the whole of a large room ".

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[*] " It was on . . . February 12, 1809 that the other man who along with Charles Darwin was most profoundly to influence their time, and perhaps the future, was born—Abraham Lincoln " (Moore, 1955).

[†] See, for comparison, Walter Sullivan's articles about the *Atka* expedition to Antarctica in preparation for International Geophysical Year, 1957, in the *New York Times*, January–March, 1955.

[‡] Some 37 years after the discovery of the famous Kentucky Blind-fish, *Amblyopsis spelaeus*, whose origin the National Geographic Society states in 1955 " . . . is a mystery to naturalists ".

[**] Edward Whymper, 1840–1911, English Alpinist and wood engraver, who found a route up the Matterhorn in 1865.

The London *Times* for 1879 also contains numerous articles on science and natural history and makes reference to many familiar names. Thus FRANK BUCKLAND* and SPENCER WALPOLE published a report on the Sea Fisheries of England and Wales about which it was written:†

> On these very surfaces and in these very depths there rages, has ever raged, and ever will to the end of time, a warfare compared with which historical battles sink to the dimensions of street rows or family jars. It is an incessant and universal war carried on between greater numbers than can be told, more species than can be well distinguished one from another, and every order of existence, from the scarcely visible and scarcely animated fibre or molecule up to the lords of creation. . . . Fish engaged in a universal internecine war devour many times more than we can do.

FRANCIS DAY‡ read a paper to the Linnean Society on the instincts and emotions of fish. EDWIN RAY LANKESTER, founder of the Marine Biological Association five years later, was Public Examiner in Natural Science at Oxford. EDWARD COPE was appointed head of the department of organic material of the Permanent International Exhibition of Philadelphia. ALEXANDER AGASSIZ was chief of the scientific staff on the cruise of the *George S. Blake* through the West Indies. WILLIAM B. CARPENTER resigned as Registrar of London University; this was the man who had helped to induce the Admiralty, through the Council of the Royal Society, to place at his and WYVILLE THOMSON'S disposal first H.M.S. *Lightning* (1868) and then H.M.S. *Porcupine* (1869 and 1870) for deep-sea exploration (THOMSON, 1873), and who was a prime mover with the Government for the *Challenger* expedition " . . . to explore and make known the conditions of life in the great oceans " (HERDMAN, 1923). HUXLEY received an honorary LL.D. from Cambridge in company with ROBERT BROWNING. And at younger levels, WILLIAM HERDMAN received his B.Sc. and the

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* Author of *The Natural History of British Fishes*, London, 1880.

† London *Times*, December 6, 1879, p. 9.

‡ Author of *The Fishes of Great Britain and Ireland*, two volumes, London, 1880–1884, and of *British and Irish Salmonidae*, London, 1887.

Senior Bursary in anatomy and physiology from Edinburgh, while the Junior Mackenzie Bursary went to one D'Arcy Wentworth Thompson for " . . . the greatest industry and skill in the particular anatomy work during the winter session ". Francis Maitland Balfour, 1851–1882, had just published his monograph on the *Development of Elasmobranch Fishes*.[*] German carp were introduced in southern United States waters, and the previous year the U.S. Fishery Commissioners had " . . . made a present of a million ova of the California salmon . . . to the Government of New Zealand ", about 95% of which were reported to have produced " healthy fish ".[†] Over 100,000 individuals were employed directly or indirectly in the Scottish fisheries, and the Herring Board stated that:

> With the exception of the occasional and uncontrollable influences of the weather which cause temporary fluctuations in the catch, the sea fisheries of Scotland and the herring fisheries in particular, are beyond the reach of any power to impair their abundance.

The British Association Meetings for 1879 opened in Sheffield on August 20th, and Professor G. J. Allman chose for the subject of his presidential address, " An Account of the Most Generalized Expression of Living Matter ". He made particular reference to the grey gelatinous material which appeared in preserved samples of the deep-sea dredgings made from the *Porcupine* at depths of 5,000–25,000 feet, and of the fact that it had appeared to be " . . . obviously endowed with life ". He recounted how it had been examined by Huxley, who declared it to consist of protoplasm and envisaged this living slime as extending over wide areas of the sea bottom as a sort of pabulum on which the animals living at these depths fed in the absence of plant life. Huxley had named the material *Bathybius haeckelii*, and Haeckel had fully supported Huxley's conclusions. Allman went on to state that the reality of *Bathybius* had not been universally accepted and that the *Challenger* did not find it. It remained for J. Y. Buchanan, *Challenger* chemist, to prove that the material was an inorganic precipitate owing to the action of the preserving fluid, alcohol. Huxley, in thanking Allman at the conclusion of his address, admitted that he had christened *Bathybius*. " He had hoped, indeed, that his young friend Bathybius would turn out a credit to him, but he was sorry to say as time had gone on Bathybius had not verified the promise of his youth " (London *Times*, August 21, 1879).

. . . . .

This was the great early period of oceanography. Wyville Thomson's cruises on the *Porcupine* and the *Lightning* in the North Atlantic had destroyed Edward Forbes' conception of the azoic zone. In 1870 Thomson, now forty, and having spent seventeen years teaching in Ireland, succeeded Allman in the Chair of Natural History at Edinburgh. The *Challenger* expedition followed, with Thomson as director of the civilian scientific staff on board. As Murray (1895) reports, " After circumnavigating the globe, and carrying on deep-sea and other investigations in many regions of the ocean, the *Challenger* returned to England in May 1876, and the crew was paid off after the ship had been in commission for over three years and seven months ". Then came the question of how best to work up and publish the results. Quantities of data in all branches of oceanography had been recorded, and the collections, which had been sent back to England from the expedition's different ports of call or brought back on ship-board, were wonderful in their extent and variety. There was extensive correspondence, in which members of the Royal Society, the Admiralty, the British Museum, and the Treasury all had a hand. MURRAY (*loc. cit.*) again writes, " It was further determined that the records of the various observations and marine collections should remain in the meantime in the hands of those who had taken part in the Expedition, and that a temporary Government department, with a small annual grant, should be created, the duty of which should be to direct the discussion of the physical and biological observations, the examination of the collections, and the publication of the scientific results, so far as these had a bearing on the science o Oceanography ". Her Majesty's Stationery Office was to publish the results, and the " typical collections " were eventually to be deposited in the British Museum. In 1877 WYVILLE THOMSON was appointed Director of the *Challenger* Expedition Commission, with headquarters in Edinburgh and JOHN MURRAY as first assistant. WYVILLE THOMSON fell into ill health shortly thereafter, and he lived only five more years—to the age of 52. In that time he settled the style of the publications and sent " a considerable part " of the collections to the specialists* who were to examine and describe them. In fact, by 1882, the year of his death, 22 of the *Challenger* Memoirs were in print, the first having appeared in 1880. It remained for MURRAY to see the job through; the last of the " Fifty large Royal Quarto Volumes " appeared in 1895.

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[*] Macmillan and Co., London, 1878; reprint of papers in the *Journal of Anatomy and Physiology*, 1876–1878. The present-day classics on Elasmobranchs are by Bigelow and Schroeder (1948 and 1953).

[†] At the same time the question of introducing California salmon into British waters was the subject of much debate in England. One writer, Sir Rose Price, emphasized the " . . . extremely risky nature of the experiment ", and claimed these fish would not take a fly and had no flavour. He concluded by stating, " The mortality among salmon in California is simply incredible " (London *Times*, April 16, 1879).

THOMSON'S letters to GÜNTHER† resulted in three memoirs: on the shore fishes (1880), on the deep-sea fishes (1887), and on the pelagic fishes (1889). The correspondence, not all included here and in a most unhappy long-hand, provides fair evidence of the tremendous pains to which Sir WYVILLE went, of his attention to detail, of his ability to prod the contributors to the *Challenger* Reports when occasion demanded, and of his insatiable desire to see the whole series done to the highest degree of perfection.

University—Edinburgh
March 17, 1877

Dear Dr. Günther:

We have now gone over the greater part of the " Challenger " spirit collections and the Fishes are nearly ready to be handed over to you if you are inclined to take them up.

There are two distinct sets—those from the shallow water and from the marshes. This collection is not large as such a collection might easily be made with more time but I have no doubt there are many undescribed forms from the more remote places.

The other set is from deep water and many consist of a couple of hundred specimens (more or less) of forty or fifty species of which a large proportion are undescribed. They are mostly allied to the deep-water things which have come home from about Madeira.

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* The completed *Challenger* Reports contain contributions from 76 authors.

† Published with the permission of the Trustees of the British Museum. We here express our best thanks to the several persons who helped us with the original letters of C. WYVILLE THOMSON in the B.M.N.H., particularly Mr. MUGFORD of the Mineralogical Department Library.

If you undertake the Fishes the arrangement approved by the Treasury and by the Trustees of the British Museum is the following.

"That the fishes be sent to Dr. Günther for determination and description and that Dr. Günther be requested to select a complete set for the British Museum including all unique specimens and two specimens of all species of which there are more than three; the remaining duplicates to be returned to me for distribution with the sanction of their Lordships."

There is one point with regard to the deep-sea fishes especially which I must mention. Mr. Murray has had charge of these and has devoted special attention to the circumstances under which they have occurred making careful notes in each case. No description would be complete particularly in its bearings on physical geography without such information and I think it would be very desirable that Mr. Murray should be associated with you in the description of this section; this is a matter, however, which I must leave in your hands.

I should wish all new species and all species which have not already been well figured in readily accessible publications to be fully illustrated with any necessary anatomical details. Of course I am prepared to defray the expense of illustration. I should like, if possible, to have some at all events of the plates done during the next financial year and I would be greatly obliged to you if you would, when you see the specimens, give me a rough estimate of the number of plates which will be required and of the approximate costs.

In the meantime, will you kindly let me know your views generally on the matter and when you would wish the Fishes sent.

I enclose a proof of a list of observing Stations and will send a corrected copy with the chart shortly.

I send a rough proof of one of the plates to give the size.

Yours faithfully,
C. Wyville Thomson

Bonsyde
*Linlithgow, N.B.**
July 10, 1877

Dear Sir:

I do not think that there is the slightest objection to your publishing the Kerguelen Fishes in either way you prefer—Annals or Phil. Trans. The deep-sea series I should think of course to form a part—or volume if need be—of the official report. Would you be good enough to give me so far as you can a rough estimate of the amount which you expect to be able to undertake—plates and letter-press, during the current financial year, and the total expense for this year—the plates on the stone and the letter-press ready to go into the printer's hands.

I am glad that you are finding so many new and interesting forms. I think you may depend upon the condition of the specimens being good, for certainly no care has been spared either in that or any other group of marine forms.

I am yrs faithfully,
C. Wyville Thomson

University of Edinburgh
18 *October*, 1877

Dear Sir:

I now enclose a plate as a sample of size and style that we may have the whole series as nearly uniform as possible. The tinting, the additional expense for which has been sanctioned by the Stationery Office, gives a great advantage in brightening of the figures by the use of white.

The exact size of the tinted portion of the plates, well within which the figures must be kept, is 10 × 8 inches. It would be well to keep the lettering the same as on the sample plate, altering the legend on the right hand upper corner as required, e.g., Foraminifera Pl. III Ostracoda Pl. IV.

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* Thomson's ancestral country home, where he was born and where he died. The centre window of the apse of the parish church of St. Michael of Linlithgow was done in 1885 in memory of Sir Wyville; the subject is a representation of the 104th Psalm, God's manifestation of Himself in the Works of Creation, and in the lower parts of the window are illustrated the "great and wide sea".

I should like that two proofs of each plate should be sent to me before the requisite number of impressions, which will probably be 525 are printed off.

The paper will be supplied by the Stationery Office. I am, sir,

Yours faithfully,
C. WYVILLE THOMSON*

Edinburgh
November 13, 1877

Dear Dr. Günther:

I have written to Spence Bate.† Under all the circumstances it may perhaps be as well to allow the Brachyura to stand over for the present.

Will you kindly let me know for the information of the Stationery Office how you propose to have your plates lithographed—through what firm, and at what cost—the plates to be of the same size as the pattern plate sent and the number of copies probably about 730. The Stationery Office supplies the paper, so it is merely the use of the stones and the printing.

Thank you for your interesting account of our Japan species. What a number of new forms there seems to be. Believe me.

Yrs. faithfully,
C. WYVILLE THOMSON

Edinburgh
May 4, 1878

Dear Dr. Günther:

I should think that there cannot be the least doubt of the advantage of the course you propose. The abstract of the description in the Annals should be " published with the permission of the Lords Commissioners of the Treasury ". I have heard nothing about fishes from Agassiz. He has got a fine haul of invertebrates.

Let me know what arrangement you make when you begin the plates so that we may be all square with the Stationery Office.

Yours faithfully,
C. WYVILLE THOMSON

University
Edinburgh
July 5, 1878

Dear Dr. Günther:

Thank you for the signed list. It keeps things all square.

I am very glad to know that the illustrations of the Fishes are going on.

I am glad also that the condition of the Fishes pleases you. Murray took a great deal of trouble.

Yrs. faithfully,
C. WYVILLE THOMSON

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* This letter is not in THOMSON's own hand, though the signature is clearly his.

† See *Challenger* Report on the Crustacea Macrura, Vol. 24 (Zool.), Pt. LII, 1888.

Edinburgh
October 12, 1878

Dear Dr. Günther:

I am delighted to see the plates. They seem to be excellent. We have a contract with Mintern's so all you have to do is to order from him is to order (*sic*) 750 copies of each plate on the terms of his contract for the Challenger work. I think the best plan would be to leave all the plates at Mintern's except 20 copies of each which are allowed for editorial purposes, and which I should like to have sent to me. I do not care to have all the plates stored in one place. It concentrates the risk too much. I suppose Mintern's people have a fire-proof store. The faster the plates come in now the better. I fear it will be *impossible* to complete the whole work within the time I gave*—but—we are doing our best.

I send a copy of Lyman's synopsis of the first division of the Ophiuroids so you see what you have to expect in the way of new forms. I have not yet got the type specimens of the Echinids but most of the plates are done so you will get them soon.

Believe me

Yrs. faithfully,
C. Wyville Thomson

Edin.
December 31, 1878

Dear Dr. Günther:

Of the enclosed documents those marked I and II were returned to me from the Treasury on the grounds that Plates 3 and 6 had been charged twice.

I had signed both accounts supposing that the double marks referred to the two series—shore and deep-water fishes. Mintern's people seem to be careless in these matters. If this is the second time a mistake has occurred, would you mind asking them to send their accounts to you and initialing them if you find them correct?

Yrs. in this
C. Wyville Thomson

Edinburgh
January 25, 1879

Dear Dr. Günther:

Will you very kindly try and fill up the accompanying sheet. I am anxious to make out as clearly as possible where I am and what I may expect.

Yrs. faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
Nov. 12, 1879

Dear Dr. Günther:

I am now going on with your report and I will send you some proofs in a few days. It is somewhat different in form from the others. I thought the plates had been printed off. I suppose Mintern had better send to me a demand for the paper they require and I will send it up to the Stationery Office.

Will you kindly let me know to what the *numbers* attached to the species of shore-fishes refer.

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* Murray (1895) writes, " In the year 1889 Her Majesty's Treasury declined to ask Parliament to renew the annual grant for the continuation of the work relating to the scientific results of the Expedition the time estimated for the completion of the publications having expired. However, after some correspondence, in which I offered to finish the Report at my own expense, the Government agreed to set apart the sum of sixteen hundred pounds for the completion of the official publications in the same style as that in which they had hitherto appeared. This sum has been the only payment from Government funds in connection with the Challenger Expedition during the past six years. . . "

As to the pelagic fishes if you think they would be better on woodcuts I have no objection. If you can employ Mr. Cooper 188 Strand to cut the blocks it would be convenient as we shall have an account with him at all events.

I shall be very glad to see the deep-sea fishes. Of course in this report the interest centres on the distribution and the bathymetrical range of the forms, and I should like it to be as complete in this respect as possible so as to form a basis for future work.

I would be glad if you would kindly give very full lists of the deep-sea fishes which have been described hitherto, and if you would cause to be figured anew any species taken by us, which have been only described and not figured, which have been badly figured, or which have been figured in not easily accessible books. You are no doubt aware that Agassiz's deep-sea fishes are in Steindachner's hands and now well advanced. As the abyssal fauna is very uniform many of our species are in that series.

I have heard from several of your London acquaintances that you are in some way dissatisfied with the form in which you are receiving the British Museum Series of specimens. I do not know what the cause of complaint is, but if there be any it would be better perhaps to refer it to myself. I send a proof which happens to be lying before me to show you the form which the reports are taking.

Yrs. faithfully,
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
Nov. 17, 1879

Dear Dr. Günther:

Thank you so much for your note. You have not however told me to what the nos. attached to the Shore-fishes in your list refer. Please let me have a post-card as soon as you can.

I assure you if I had only heard of your supposed dissatisfaction casually or from one source I should have said nothing about it. Since, however, there seems to have been some mistake there is no use in taking further notice of the matter.

I consider it perhaps the principal part of my duty in connection with the working up of the "Challenger" collection to place the *type specimens* and whatever else seems necessary for full illustration, of every species, in the British Museum. And this I will carry out to the best of my power. As I told you at the time the specimens which you got from Agassiz belong to known species, and to a few new species of which many samples were found—possibly some of them are unnamed, and I sent them to you just as they came as I am aware that each transfer however carefully managed does some little damage, and I did so mainly that some pretty things such as Coelopleurus, Salenia, Asthenosoma, etc., might be seen at once.* You will get the type specimens whenever they are figured and described.

Thank you for your kind reference to my late illness. I fairly broke down with over-work, but I am now nearly as well as ever.

Believe me

Yrs. faithfully,
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
Feby 13th, 1880

Dear Dr. Günther:

I send you at last a proof of your report on the Shore-fishes. I thought you would have had it long ago but some other things occupied us very fully for a time. As it turns out however this delay has been of no consequence for it will be a month yet it seems before your plates are printed off.

What I send you, then, is a first-proof, corrected as far as we could manage it, but still needing to be put into shape in certain respects. The Geographical list* I propose should come first—as an elaborate Table of contents. Then the descriptions and the systematic list at the end. There are several mistakes and among them a few which ought to be corrected. For example the fresh-water fishes from the Mary river were not presented to us but caught with some labour by a little party consisting of Murray, Lieut. Aldrich, and myself, who squatted on the bank of the river for a fortnight in the hopes of getting young *Ceratodus*. We took two of the mature Ceratodus however and it should have been in your list. The specimens were not sent to you as they were not put up with the rest of the fishes. I know you had plates of it so I suppose you do not wish them. If you do you can have *one*. I should like to keep the other here as a memento of a pleasant holiday trip.

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* See *Challenger* Report by A. AGASSIZ, Vol. 3 (Zool.), Pt. IX, 1881.

To save you trouble it would be better perhaps that I should add when necessary a note indicating anything special about the fishes—such as the mode of preserving them at different places. The account is rather bald without a few such details.†

Would it not be as well to substitute some other specific name for *Sancti pauli*.‡ The French are just describing the fauna of the other St. Pauls which is so much better known.

In the introduction of your preliminary notes on the Deep-sea fishes you make some remarks as to the extent and condition of the collection of fishes. I suppose you have no objection to these remarks being repeated here.

I send you two copies of the proof. If you want additional copies please send me a line—also if it is necessary to send the Mss. I retain a copy and will add such additional notes as I think are necessary, and then, when I get your corrected copy, I will have a clean proof drawn and send it to you before printing off, in case you have any further alterations.

I will be glad of the deep-sea fishes whenever I can get them. The first spurt is about over and we shall need as much material as we can get to go on with.

You will get the type collection of the Echini very shortly now. I hear from Agassiz that he is very nearly done. I hope to be able to be in London in March but I am not quite strong yet and am shirking the journey as long as possible.

Yrs. faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
February 24, 1880

Dear Dr. Günther:

I am afraid it was trespassing altogether too much upon your time to ask you to take charge of the Report on the Challenger Fishes, but I followed the principles I tried to work on as far as I could, and applied to the most distinguished Ichthyologist I knew. I must ask you however to allow me to bring your list as nearly into the form which has been adopted after much consideration for the report, as its nature will allow.

I am taking the utmost care that the type collection of everything goes to the British Museum in its thorough completeness but I do not mean to make the Challenger Report a Museum Catalogue in any sense. The data I mean to publish are those which have reference to the Expedition. No doubt all the letters and references to specimens in and out of the Museum will appear in your own catalogues when these Fishes are added to them. Such a list as you send me should be published by the Museum if it is required.

I suppose that the Shore-Fishes are not of much importance but I do not wish to publish matter which from my point of view is wholly irrelevant, and I must add a few notes about the

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* No geographical list as such appears in the printed version; the descriptions are made under broad geographic headings, Atlantic, Temperate Zone of the South Pacific, etc.

† To make the account of *Ceratodus* less " bald ", Sir Wyville, who evidently felt strongly about these fish, wrote what must surely be one of the longer footnotes in ichthyology—almost a thousand words (Günther, 1880).

‡ Günther apparently disregarded Thomson's suggestion, for *Holocentrum sancti pauli*, n.sp. appears on page 4 of his Report on the Shore Fishes (1880).

Ceratodus and means by which the fishes were procured — to do my duty fairly as Editor. I have not time for many, but what are added you will see before they are printed off. The report on the Shore-Fishes might be as good as that on the birds which will give all the information we have. I will send you tomorrow the Mss.—and you will see that we have taken no little trouble correcting spelling, adding authorities, etc., etc. I would have certainly left out that long Geographical list altogether. It seems little more than a repetition of the main list. I will leave it out yet if you have no objection for I do not think it improves the appearance of the paper.

I have not the proof at hand—it is at the Office in Town but I will see it tomorrow and write again what I think had best be done.

Yrs faithfully,
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
March 10, 1880

Dear Dr. Günther:

I daresay your plates are now nearly finished and the rest of the volume is ready. All you need to do is to correct any errors in spelling and so on in the text, and I would like to have it as soon as convenient.

Yrs. faithfully,
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
March 22, 1880

Dear Dr. Günther:

I must apologize for having entirely forgotten to send *Ceratodus*. I suppose you have been waiting for it before sending the corrected proof. I will be glad of the proof whenever you are ready for we are anxious to set the type free.

There is another little matter which I ought to mention. I see you have communicated a paper to the Linnaean Society on some of the deep-sea fishes. If any report or abstract of that paper is published I would be greatly obliged if you would add to the heading " Published by permission of the Lord Commissioners of the Treasury ".

Of course in making this request I am only obeying my own instructions from the Treasury.

Yrs faithfully,
C. WYVILLE THOMSON

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29 *March* 1880

Dear Sir Wyville:*

The specimen of Ceratodus arrived safely on Saturday last, and I return it today with the proof sheets.

The proofs are corrected with the exception of 1. The Geographical List which you propose to leave out. I see no objection to it and only regret that it was set up in type, time and expense being thereby saved. 2. Of the enumeration of the specimens of each species which I have left as you have had it set up.

With regard to my discourse at the Linnean Society, it referred to results of examinations made by myself long ago or others more recently independently of the Challenger Collections.

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* This unsigned letter, much emended, appears to be the first draft of GÜNTHER'S answer to THOMSON'S of March 22, 1880.

Bonsyde
Linlithgow, N.B.
April 1, 1880

Dear Dr. Günther:

Many thanks for the corrected proofs. They will be put in hand immediately and I will send you a second proof before the paper is printed off. I see most of your corrections refer to matters of *form* rather than Ichthyology. I do not suppose you attach much importance to the relative positions of n and sp! Our way of putting it was adopted after an amount of consideration sufficient for the subject, I think. It means either " new species " or " nova species " as you choose. On what ground it should be inverted, unless it came in as part of a Latin sentence, I am not aware. The single i terminating proper specific names ending in a consonant is in accordance with the " Strickland Code " and is I believe correct.

The first Zoological volume will now be out at once. I have not yet got your plates from Mintern's however—but I suppose they are ready.

I suppose you will have no difficulty in arranging the account of the deep-sea fishes zoologically and putting the report into the same form as the others. It will save a deal of trouble. The sooner I can get the reports, the materials for which have been long in the hands of the authors, into print the better—for there will be a great accumulation towards the end.

Yrs faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
May 4, 1880

Dear Dr. Günther:

I hope this will answer now. I have, as you suggested, taken out the reference to the B.M. Catalogue, and have made the Report more comparable in shape of the rest.

I trust you will not find it to require much more correction—and that you will be able to let us have this Mss. proof at once, for the *succeeding* volume is almost finished and (we) are greatly pressed to put the first out of hand.

Yrs faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
May 6, 1880

Dear Dr. Günther:

I think the addition of the paging to the systematic list would be a great improvement. I would have had it done here but our hands are *very* full.

Delighted to hear that we shall soon see some deep-sea fishes.

Yrs faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
July 5, 1880

Dear Dr. Günther:

I was unlucky in missing you the last time I was in London.

You wrote me some time ago that I might expect within a very short time some of the plates of the deep-sea fishes. Could you drop me a line when you think these will be ready. I wish to arrange for the next set of volumes and I want to know when your memoir will come in—as one of very great interest.

Have you unpacked or incorporated or done anything with the set of Echinoderms I sent you? I find that they were sent in a certain sense by mistake, and I could select your full set much more satisfactorily if I had them back again. I have had no official receipt for them. They were only meant in a provisional lot in case anyone wished to see them and if they are not exhibited or entered if you wish to send them back to me I will send you the type lot complete.

Yours faithfully,
C. WYVILLE THOMSON

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*I am sorry that there has been any mistake about the preliminary set of Echinids; but, re-reading from letters, I must acquit myself of any share in the error.

The specimens have not only been put into different bottles, but have been registered, incorporated and reported to the Trustees; and by them to the House of Commons.

It is now, therefore, impossible for me to acquiesce in your request that they should be returned. It seems to me that the best thing to do will be to send me the type-series, when I will have them compared with what have been already sent, and, if I find that it is possible to return any of the freshly sent specimens, or finding that the characters and distribution of the species collected is already well enough represented by the previous series, I will certainly do so, in order that they may form a part of a good set for the museum, which has the second claim on this National collection.

So far as the specimens already sent are concerned, I may add that the assistant in my Department who is especially charged with the care of this group has engaged himself to remain in London until the end of August, and I may safely promise for him that he will spare no trouble in giving all assistance in his power to the artist (2) or the describer (1), if they are desirous of having another examination of the specimens already in the British Museum.

Bonsyde
Linlithgow, N.B.
July 10, 1880

Dear Dr. Günther:

I am greatly obliged to you for the proofs which are already in the printer's hands.

Yrs faithfully,
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
July 15, 1880

Dear Dr. Günther:

Thank you so much for your note and for the first deep-sea fish plates. I suppose in these plates you will simply put the name of the Fish beneath as we have done in the other groups without locality or anything further. Either the generic name only or the generic and specific as you think proper.

It is all right about the Echinoderms. I thought it very possible you had incorporated them. I daresay you could without much trouble send me a list of the species already sent. I think I kept a duplicate list but I have changed my Secretary since, and I cannot at this moment lay my hands on it. I want to be sure that you get every species the old as well as the (*sic*) those not previously described.

Yrs faithfully
C. WYVILLE THOMSON

P.S. Can you readily send me by return the date when you got the shore-fishes and the date when you returned me the Mss? It has been suggested to me that these should be published in all cases and I did not think of it at the time.

C.W.T.

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* This letter, unsigned and undated, but in the same hand as that of March 29, 1880, is apparently a first draft, GÜNTHER to THOMSON.

Bonsyde
Linlithgow, N.B.
October 1, 1880

Dear Sir:

I have forwarded your note to Dr. Sclater* and see no reason why you should not enter the birds in your forthcoming volumes.

The Pteropods are not even commenced. They are not so numerous as might be expected in the Collection and, as they are greatly scattered on slides and in bottles of tow-net matter, it will be some time before they are ready. We must get through with the *bigger* things first.

You will get probably tomorrow or next day, a lot of fishes from the deep water off the Faroes (?) some of the spoils of the *Knight-Errant*.† I will be greatly obliged to you if you will simply add them to the Challenger things . . . (?) That is look them over keep what you require for the Brit: Mus: and return us the remainder named. Only it would be a great favour if you would keep this lot separate, send us a specimen of all of those of which there are two in the same condition, and let me have a separate short report on them for a paper on the Faroe Channel which I am going to read at the R.S.E.

You will get lots of things in other departments by degrees from the same cruise, but I am having them all named and worked up with the Challenger things in the mean time.

Yrs faithfully,
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
October 25, 1880

Dear Dr. Günther:

Dr. Sclater promises to send you the birds as soon as possible after his return home.

I am looking out most anxiously for the plates of the deep-sea fishes. They are now pressing me to finish my work on the Collections and leaving such a crush of printing for the end that I hardly see how I can manage it.

I would prefer having, as in other Memoirs, the name of the Fish only on the plate. I would especially rather not have the depth—for although of course the depth of the sounding is given in the station for the Fish, we can seldom be absolutely sure that the fish actually came from that depth—particularly in the case of using the trawl.

Yrs faithfully,
C. Wyville Thomson

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‡The bathybial Fish-fauna which surrounds the British Islands was hitherto almost unknown. Beside the stray specimens which now and then were found thrown ashore or floating on the surface no further evidence of the existence of this fauna was obtained, except on two occasions, viz. on a dredging-excursion of Dr. Gwyn-Jeffreys in 1867 from a depth of from 80 to 90 fathoms;* and during the cruise of H.M.S. Porcupine in 1869 from a depth of from 200 to 500 fathoms.†

*See Ann. & Mag. Nat. Hist. 1867, xx, p. 287. †*Ibid.*, 1874, XIII, p. 138.

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* See *Challenger* Report by P. L. Sclater, Vol. 2 (Zool.), Pt. VIII, 1881.

† The cruise which led to the deliniation of Wyville Thomson ridge: see Herdman, p. 55, 1923.

‡ This letter, unsigned, undated, and much emended, is in the same hand as that of March 29 and the one identified by footnote *, p. 86, and is apparently another first draft, Günther to Thomson.

Neither of these two contributions can compare as regards interest and number of specimens with the series obtained during the cruise of the " Knight-errant "; and it would seem as if now only the rich spoil which I ventured to indicate in 1867 as resulting from an exploration of the Deep Sea round the British Islands, were being gathered. Six out of the ten species obtained, are new to the British Fauna; and of course represent but a small fraction of the actual number of Brit. deep-sea fishes. Much, therefore, remains to be done. The laws which govern the bathymetrical distribution of Fishes, are still obscure; and it is evident that a series of continued methodical observations, such as can be made in a limited oceanic district like that round the Brit. Islds., whose hydrographic conditions with its surface and coast fauna are so well known, is most likely to reveal a chain of facts which cannot be recognized in disjointed observations made at distant localities. Besides, there are not a few obscure points in the life-history of our food-fishes which may be well expected to be cleared up by the deep-sea-dredge, such as the unaccountable disappearance from certain parts of the coast of fishes like the Haddock, the change of habitat of many fishes according to the season, a change which evidently much more frequently takes place in a vertical than horizontal direction, etc. It is therefore to be hoped that the present successful expedition will be followed by equally well conducted efforts.

The collection submitted to my examination contains a much greater proportion of arctic forms, than of southern; and in this respect differs entirely from that made by Mr. Gwynn-Jeffreys at a less depth. The only southern form is *Haloporphynus lepidion* which we knew previously from the Mediterranean and Japan. Singularly, again, no trace of a Trachypterus or Regalecus was obtained; and we can account for their absence only by the supposition that it is difficult to enclose these long snake-like fishes in the dredge, and that young specimens from their extreme delicacy of structure are probably torn into fragments or lost long before the net reaches the surface. Some of the species have been previously obtained by the Scandinavian Expeditions in similar latitudes. As all the species will be fully referred to or described in my Report on the " Challenger " Deep-sea-fishes, only a few notes on them are appended here.

Bonsyde
Linlithgow, N.B.
Oct. 26, 1880

Dear Dr. Günther:

I had written you a note just the post before I got yrs. I am very much obliged to you for the report and greatly pleased that the fishes have interested you so much. I have been long looking forward to a careful overhaul of the Faroe Channel, and I have every hope that we may have another investigation this next summer under more favourable conditions.

So far as this years work is concerned I am at liberty to ask you to make what use you choose of the duplicity which I have much pleasure in doing (?)—only send me back what you can spare

Yrs faithfully,
C. WYVILLE THOMSON

Nov. 1*st* (?)—no address

Dear Dr. Günther:

I have just received a list signed by you from Mr. Moseley. You will exercise your own discretion in selecting the Brit: Mus: set. Of course my prime object is to make that as complete as possible, but, that done, it would be a convenience for (me) to have as many species here for comparison as I can get.

I have a note from Dr. Sclater that he has handed over or is about to do so, the birds. I suppose you will send me a list. I expect to send off the Pennatulida the end of the week.

For some whale bones and seal bones you will have to wait till the part on the bottom deposit is finished. I am *anxiously* looking for the deep-sea fishes.

This is a most laborious job!

Yours faithfully
C. WYVILLE THOMSON

Bonsyde
Linlithgow
Nov. 2, 1880

Dear Dr. Günther:

From having heard nothing from you with regard to the Corals of the *Challenger* Expedition I suppose I am right in concluding that you have not received them yet from Mr. Moseley. As some difficulties have arisen in this department I have asked Mr. Moseley, to avoid any further complications, to send *the whole collection*, the type specimens, the second selected set, and the duplicates to you. I will be very much obliged to you if you will kindly select the first set according to the instructions sanctioned by the Treasury—and return the rest to me.

I am sorry to give you this trouble—but this is I think the only case. I will send you in the course of a few days the Ostracoda and the Pennatulida. I mean in all cases to send the specimens to the Museum as soon as possible after the Memoirs are published. It would be scarcely fair to do so much before.

I have been reading your book on Fishes with much pleasure, and I think I know more about them then I did before. It is a resumé which was much wanted.

Yrs. faithfully
C. Wyville Thomson

Bonsyde
Linlithgow, N.B.
December 17, 1880

Dear Dr. Günther:

I know pretty well all about the advantages of complete collections for reference. I am only very glad that so much attention is now being paid to these minute (?) groups in the B.M.

My great object has been to make the collection from the " Challenger " in all branches in the National Collection as perfect as possible. Beyond a certain point I cannot force this but I will do the best I can.

Believe me yrs faithfully

C. Wyville Thomson

P.S. I will send you today the whole of the remaining material returned by Dr. Brady as duplicates. I forwarded your letter and list to Dr. Brady.*

Bonsyde
Linlithgow, N.B.
January 16, 1881

Dear Dr. Günther:

It has been suggested to me that perhaps I ought to have let you know that it was in my power to offer a moderate honorarium for literary work in connection with the Challenger Report. To tell the truth I had some delicacy in doing so remembering the strong representation which the Brit. Mus. officers made on that matter to government. I do not see however that preparing such a report, especially as I distinctly objected to its being in the form of a Brit. Mus. catalogue, could be considered a part of your regular work.

If you desire it I will send in an account for the sum to which you are entitled under my instructions.

Will you very kindly let me know how the Deep-sea Fishes stand.

Yours sincerely
C. Wyville Thomson

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* Either G. Stewardson Brady on the Copepoda (*Challenger* Report, Vol 8 (Zool.), Pt. XXIII, 1884) or Henry Bowman Brady on the Foraminifera (*Challenger* Report, Vol 9 (Zool.), Pt. XXII, 1884).

Bonsyde
Linlithgow, N.B.
February 11, 1881

Dear Dr. Günther:

I am extremely sorry to hear that you are still on the sick list. I hope you will shortly be in condition to resume your work with comfort again. As to future arrangements I will be glad to meet your wishes in every way, as far as I can.

Yrs faithfully
C. WYVILLE THOMSON

Bonsyde
Linlithgow, N.B.
March 1, 1881

Dear Dr. Günther:

Let me introduce to you my Secretary Dr. W. A. Herdman, F.Z.S.—from whom I think you have heard from time to time.

I will be very much obliged to you if you will let him overhaul your *Ascidians*. He is doing ours and I know that he is thoroughly up to them. If you can help him in any way you will do me a great favour. Also on all " Challenger " matters talk to him as to myself.

I sincerely hope that you are now all right again. I hope to be in Town in about a fortnight or so.

Yrs faithfully
C. WYVILLE THOMSON

Bonsyde
Linlithgow
December 4, 1881

Dear Dr. Günther:

I am getting very anxious about your paper on the deep-sea Fishes and would be very glad to see some of the work. Both the Royal Society and the Treasury are expressing some impatience and I may be landed in difficulties if some of the promised memoirs are much longer delayed.

I would be greatly obliged to you also if you would send me a receipt for the Echinoidea sent by Agassiz according to his Memoir.

There are several other Memoirs which will be ready for delivery shortly.

Believe me
Yrs faithfully
C. WYVILLE THOMSON

MURRAY (1895) speaks of the fact that the *Challenger* Reports cover " . . . about twenty-nine thousand five hundred pages, illustrated by over three thousand lithographic plates, copper plates, charts, maps, and diagrams, together with a very large number of wood-cuts ". He goes on to say, " From beginning to end the history of the Challenger Expedition is simply a record of continuous and diligent work ". In a sense it is just that. But who, most of all, had the perspective and pertinacity to initiate this first real study in deep-sea research? If THOMSON were alive today, it is fair to speculate that he would be astounded at the developments in oceanography since 1879. His was an unusually broad, inquiring mind—to which his writings and editing testify abundantly; his was the imagination that resulted in the *Challenger* Expedition; and his was the guiding hand that led to the foundation of the modern science of oceanography. In mute testimony, his name appears on the title page of all *Challenger* volumes—whether produced before or after his death—" Prepared under the Superintendence of (the late) Sir C. WYVILLE THOMSON, Knt., F.R.S., &c. Regius Professor of Natural History in the University of Edinburgh, Director of the Civilian Scientific Staff on Board".

REFERENCES

BIGELOW, H. B. and SCHROEDER, W. C. (1948), Fishes of the Western North Atlantic. Pt. 1. Sharks. *Sears Foundation for Mar. Res., Mem. I*, 59–576.

BIGELOW, H. B. and SCHROEDER, W. C. (1953), Fishes of the Western North Atlantic. Pt. 2. Sawfishes, Guitarfishes, Skates and Rays. Chimaeroids. *Sears Foundation for Mar. Res., Mem. I*, 1–588.

GÜNTHER, ALBERT (1880), Report on the Shore Fishes procured during the Voyage of H.M.S. Challenger in the Years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, etc., *Zool.*, I, 1–82.

GÜNTHER, ALBERT (1887), Report on the Deep-Sea Fishes collected by H.M.S. Challenger during the Years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, etc., *Zool.*, XXII, I–LXV and 1–335.

GÜNTHER, ALBERT (1889), Report on the Pelagic Fishes collected by H.M.S. Challenger during the Years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, etc., *Zool.*, XXXI, 1–47.

HERDMAN, W. A. (1923), *Founders of Oceanography and their Work*. Edward Arnold & Co., London, 340 pp.

MOORE, RUTH (1955), *Charles Darwin*. Alfred A. Knopf, New York, 206 pp.

MURRAY, JOHN (1895), A Summary of the Scientific Results. Editorial Notes. *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, etc., VII–XII.

RUSSELL, F. S. and YONGE, C. M. (1928), *The Seas*. Frederick Warne & Co. Ltd., London and New York, 379 pp.

THOMSON, C. W. (1873), *The Depths of the Sea*. Macmillan and Co., London, 527 pp.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 92-109.

The hydrography and the distribution of chaetognaths over the continental shelf off North Carolina

By DEAN F. BUMPUS*†
Woods Hole Oceanographic Institution
and
E. LOWE PIERCE
Department of Biology, University of Florida

Summary—Temperature, salinity and quantitative plankton data have been obtained from the continental shelf area and Florida Current off North Carolina in May and June 1953 and January 1954.

Two water types, Virginian Coastal water and Carolinian Coastal water, and one water mass, Florida Current water, are identified.

A breaching of the barrier at Hatteras between the two coastal water types was witnessed, and Virginian Coastal water was driven south-westerly across Diamond Shoals into Raleigh Bay by a north-east storm. The import of such an hydrographic event on the distribution of plankton is discussed.

The distribution of the chaetognaths in the area was investigated and their association with the water type and water mass tabulated. Twelve species representing three genera were collected. All of these are found in tropical and sub-tropical waters. Chaetognaths fail as satisfactory indicators of the Virginian Coastal water intrusion into Raleigh Bay because of the absence, in our collection, of characteristically Virginian types in the southern limits of that faunal subprovince.

INTRODUCTION

PRIOR TO the efforts of PIERCE (1953), who described the distribution of the chaetognaths over the continental shelf off North Carolina in relation to the hydrography of the area, and BUMPUS (1955), who considered the circulation of these waters, little was known about the effect of the circulation system on the distribution of planktonic elements of the flora and fauna in the Hatteras area. PARR (1933) noted in winter a temperature barrier at Cape Hatteras corroborated by BIGELOW (1933) and a fairly large cold-water temperature zone southwest of Cape Hatteras. This temperature barrier is well illustrated in the surface temperature charts of FUGLISTER (1947). BIGELOW and SEARS (1935) pointed out the abrupt transition in salinity which occurs at Cape Hatteras, occasioned by the wedge of pure oceanic water ($>35{\cdot}5$‰) which presses in close across the shelf in Raleigh Bay and entirely separates the shelf and slope water bands to the north from the low coastal salinities farther south. The data available at that time suggested that the situation exists throughout the year.

The existence of a barrier at Cape Hatteras has been postulated in defining the Carolinian and Virginian faunal subprovinces (JOHNSON, 1934). Many other zoologists have separated the cold-water and warm-water fauna on the continental shelf at this cape. WILLIAMS (1948, 1949), SUTCLIFFE (1950) and PEARSE and WILLIAMS (1951) found bottom living fauna, algae and plankton in Onslow Bay having in general tropical affinities. However, they noted in their winter and spring collections, in addition to the usual populations, a few individuals from a small number of species with northern affinities.

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* Contribution No. 760 from the Woods Hole Oceanographic Institution.

[†] Part of this research was sponsored by the Office of Naval Research under contract No 27701.

Our recent collections provide material for a better understanding of the hydrographic influence on the distribution of the chaetognaths in the area than has been available heretofore and indicate how the hydrographic barrier at Cape Hatteras is occasionally breached, thus permitting the temporary establishment of the anomalous communities noted by Williams, Pearse and Sutcliffe.

ACKNOWLEDGEMENT

While the many outstanding investigations of Henry B. Bigelow do not strictly pertain to the area under discussion, the authors are especially grateful for his studies of the waters of the Gulf of Maine and the continental shelf from Cape Cod to Chesapeake Bay. His efforts have been a constant influence as we have attempted to extend the knowledge of shelf waters slightly beyond the area he so carefully and completely considered.

THE DATA

The data comprise a series of hydrographic sections together with plankton collections made in May and June 1953 (*Caryn* Cruise 64) and January 1954 (*Atlantis* Cruise 196) (Fig. 1).

At each station serial temperature–salinity depth determinations were made to the bottom or to nearly 500 metres, whichever was less. At most stations quantitative oblique plankton tows, using Plankton Samplers (Clarke and Bumpus, 1950) fitted with #2 silk nets, were made from near the bottom or 100 metres. When feasible two Plankton Sampler tows were made dividing the water column in two. The chaetognaths were picked out of the plankton samples and identified (Tables I and II, Fig. 12). These plankton data are more nearly quantitative and extend closer to the shore than those of Pierce (1953).

HYDROGRAPHY

Bumpus (1955) has shown that, south of Cape Hatteras, a southerly flowing coastal current, such as is common north of Cape Hatteras, is a transient affair. Such a current, when present, is restricted to a very narrow portion of the continental shelf. The dynamic pressure gradient resulting from the combined effect of the runoff and the cross-shelf thermal gradient together with the prevailing wind and the frictional drag of the Florida Current provide for a northeasterly drift over a broad part of the Carolina continental shelf.

In addition to the water of the Florida Current there are two types of water in this region which we have named Virginian Coastal water and Carolinian Coastal water.* There are also mixtures of each of these with the Florida Current water. Virginian refers to the shelf water from Cape Cod to Cape Hatteras. Carolinian refers to the

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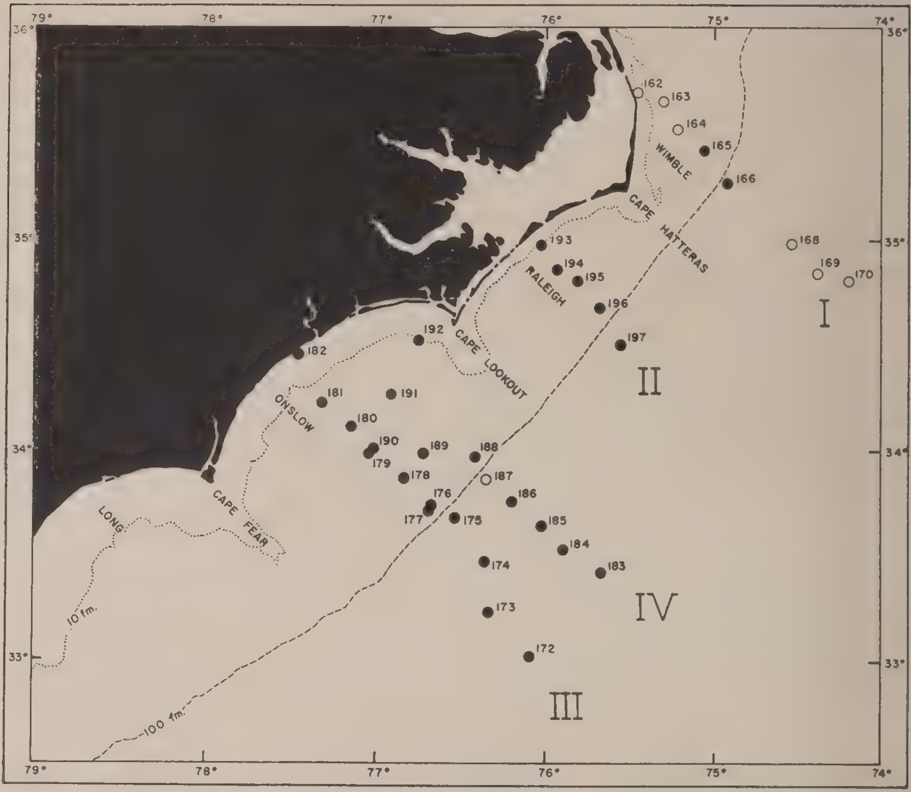
* We have used here two names apparently new to oceanography inasmuch as we have been unable to find names concisely describing the separate continental shelf regions north and south of Cape Hatteras. Because the terms Virginian and Carolinian are used to describe the faunal subprovinces of the continental shelf, we shall introduce these terms to identify the water types on the shelf.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WIMBLE
CAPE HATTERAS
RALEIGH
CAPE LOOKOUT
ONSLOW
CAPE FEAR
LONG
10 fm.
100 fm.
I
II
III
IV

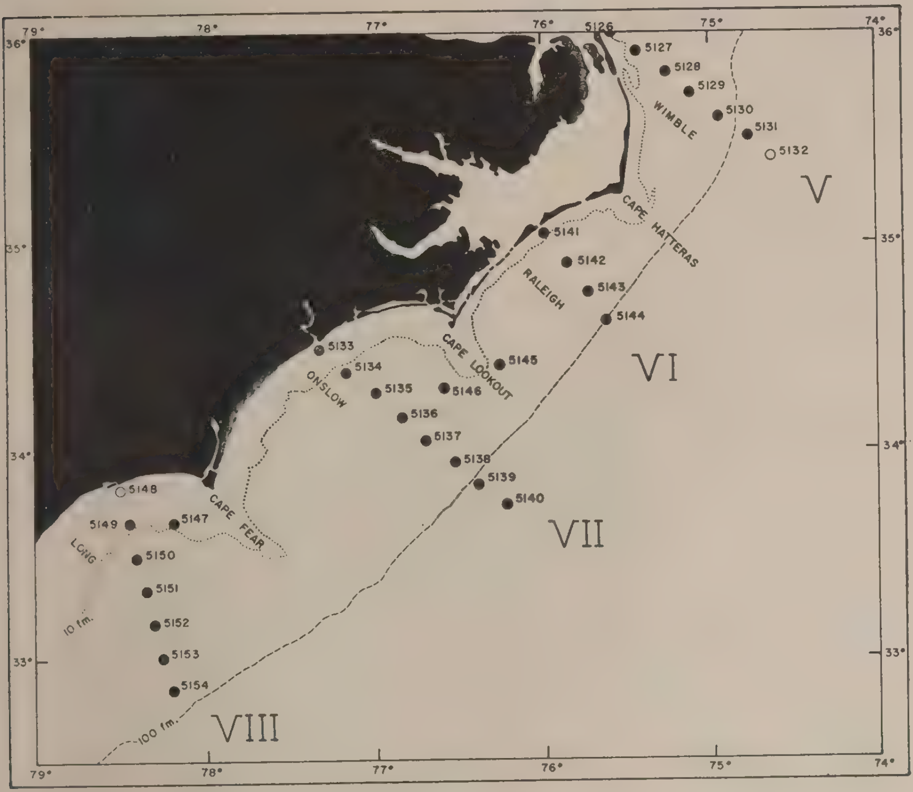
Fig. 1 (A). Location of stations, on *Caryn* Cruise 64, May and June 1953. Open circles indicate no plankton tows were made.

shelf water from Cape Hatteras southwards. Unpublished data indicate that Carolinian Coastal water, as described below, extends to the offing of Daytona Beach and possibly at certain times to the offing of Cape Canaveral.

The Virginian Coastal water is freshened by river water entering close to the surface inshore and salted by indrafts of slope water over the bottom from offshore (BIGELOW and SEARS, 1935). There is no widespread contribution to this coastal water from the south, nor flooding of the surface water with pure oceanic water of high temperature, nor upwelling onto the shelf of cold abyssal water (BIGELOW, 1933).

The Carolinian Coastal water is composed of Florida Current water and river effluent. This mixture is in general more saline than most coastal waters because the river runoff is less than for other sections of the coast; the effluent from the sounds is more saline than from river mouths; and the highly saline Florida Current frequently makes broad invasions over the continental shelf.

There is no regular communication between the Virginian and Carolinian Coastal waters, although the frequent northeast storms from November to May (MILLER,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WIMBLE
V
CAPE HATTERAS
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RALEIGH
VI
5133
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CAPE LOOKOUT
ONSLOW
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VII
5148
5147
5149
CAPE FEAR
LONG
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5151
5152
5153
5154
10 fm.
100 fm.
VIII

Fig. 1 (B). Locations of stations on *Atlantis* Cruise 196, January 1954. Open circles indicate no plankton tows were made.

1946; New York University, 1954) provide the energy for transient indrafts of Virginian Coastal water into Raleigh Bay. Three events may take place following such an indraft:

A. If the storm lasts for only a short period, one or two days, this water will eventually become absorbed within the Carolinian Coastal water, modifying it in proportion to the mixture.

B. A violent meander of the Florida Current may completely sweep the indrafted Virginian Coastal water out of Raleigh Bay toward the northeast. Such an event would be aided by a southeast storm.

C. If the northeast storm lasts for a period longer than two days or if another northeast storm follows within a few days, the indrafted water may eventually be driven around Cape Lookout into Onslow Bay. Such an occurrence could account for the presence there of the winter–spring species with northern affinities described by WILLIAMS (1948, 1949), SUTCLIFFE (1950), and PEARSE and WILLIAMS (1951). Should this occur at a time of substantial runoff when a southerly flowing coastal current is being maintained in Onslow Bay and southward, such water movements may distribute planktonic elements of Virginian fauna for some distance along the coast.

We have postulated here a sporadic occurrence which may contribute appreciably to the finding of anomalous species in the inshore waters of the northern part of the Carolinian subprovince. These species will find themselves in waters compatible to their existence until vernal warming traps them. Vernal warming or reduction in runoff with a consequent increase in salinity will kill those species least resistant to higher temperatures and salinities.

THE DISTRIBUTION OF TEMPERATURE, SALINITY AND DENSITY IN MAY AND JUNE, 1953, AND JANUARY, 1954

Typical spring conditions were encountered on the May and June cruises (Figs. 1, 2, 3, 4 and 5). These are the weak cross-shelf temperature gradient, moderate vertical temperature gradient, and the penetration across the shelf of highly saline Florida Current water along the bottom into Raleigh and Onslow Bays. In contrast the temperature and salinity in the Wimble Section are lower with weaker vertical temperature gradients and stronger salinity gradients.

Typical winter conditions for the Wimble, Onslow and Long Bay sections were observed in January 1954 (Figs. 1, 6 to 10). Note the cold coastal water in the Wimble section and the nearly as cold, highly saline water in Onslow Bay and Long Bay. But Raleigh Bay was filled in its inner part with coastal water from north of Cape Hatteras, in contrast to the typical winter conditions of January and February 1950 (BUMPUS, 1955) and February 1931 (BIGELOW and SEARS, 1935), when the 36 ‰ isohaline (Florida Current water) was pressed well in across the continental shelf. This anomalous condition was due to a north-east storm several days earlier.

This intrusion of Virginian Coastal water into Raleigh Bay is further discerned in the temperature–salinity relation (Fig. 11). The water at Stations 5141, 5142 and 5143 is clearly Virginian Coastal water.

The temperature–salinity relations also provide a clue to the sources in the Florida Current contributing to the composition of Carolinian Coastal water. The water over the inner middle part of Long Bay (Stations 5149, 5150, 5151), Onslow Bay (Stations 5134, 5135, 5136, 5146) and the southern part of Raleigh Bay (Station 5145) in January appears to be from depths in the Florida Current, i.e. from depths perhaps as great as 150 metres. This water has been forced up onto the shelf in the course of current meanders and chilled by the colder air temperatures encountered there. Stations 5133 in Onslow Bay and 5147 and 5148 in Long Bay, the closest inshore stations, indicate appreciable dilution of this Florida Current water with river effluent and greater chilling as a result of the colder air temperatures near the coast. In contrast, the water over the outer parts of the shelf (Stations 5144 in Raleigh Bay, 5137, 5138 and 5139 in Onslow Bay and 5152, 5153, 5154 in Long Bay) is Florida Current water which has moved in over the shelf with no change in depth and has mixed only slightly with the water inshore of it.

The intrusion of Florida Current water along the bottom in Onslow and Raleigh Bays in May and June (Figs. 3, 4, 5 and 11) was probably along surfaces of equal density. It has been forced onto the shelf by the meanders of the current as it passes

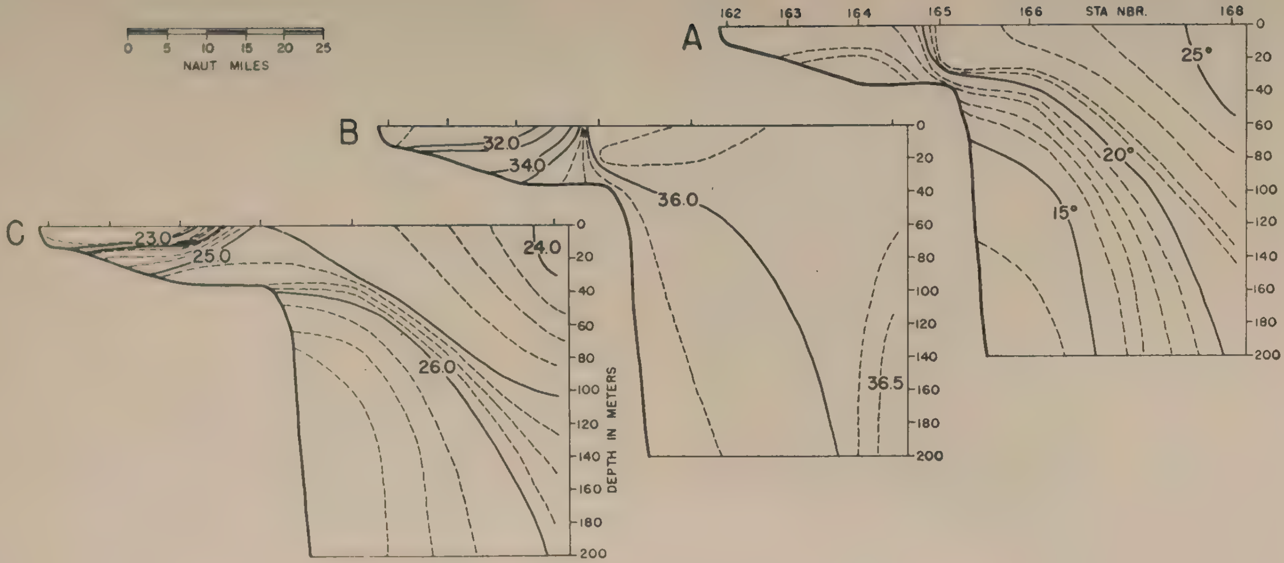

Fig. 2. (A) Distribution of temperature in ° C, (B) salinity in ‰ and (C) density (σ_t), in Section I, Wimble Shoals, May 1953.

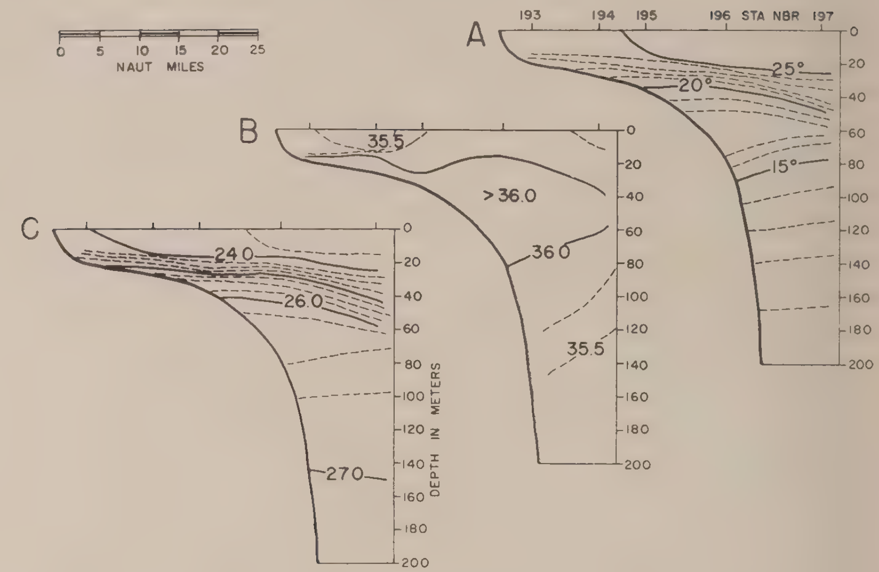

Fig. 3. (A) Distribution of temperature in ° C, (B) salinity in °/₀₀ and (C) density (σ_t), in Section II, Raleigh Bay, June 1953.

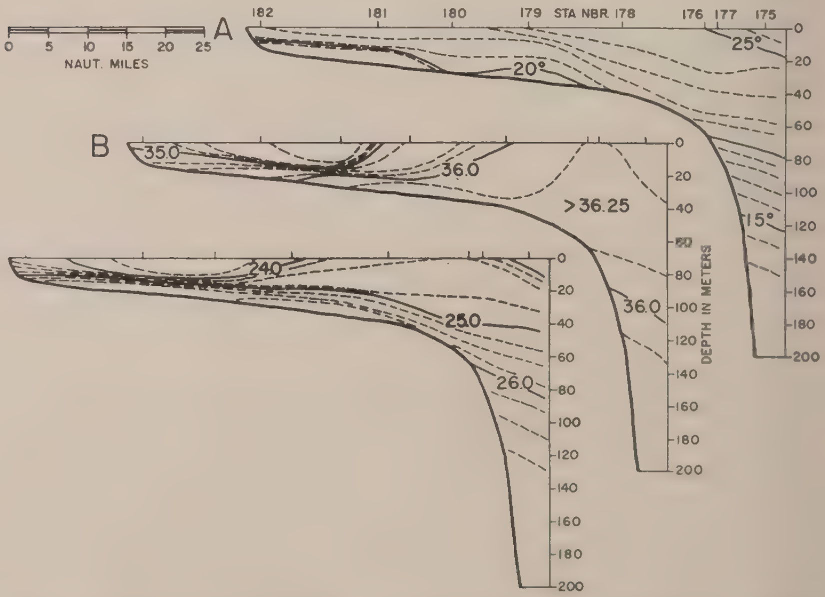

Fig. 4. (A) Distribution of temperature in C, (B) salinity in and (C) density (σ_t), in Section III, Onslow Bay, May 1953.

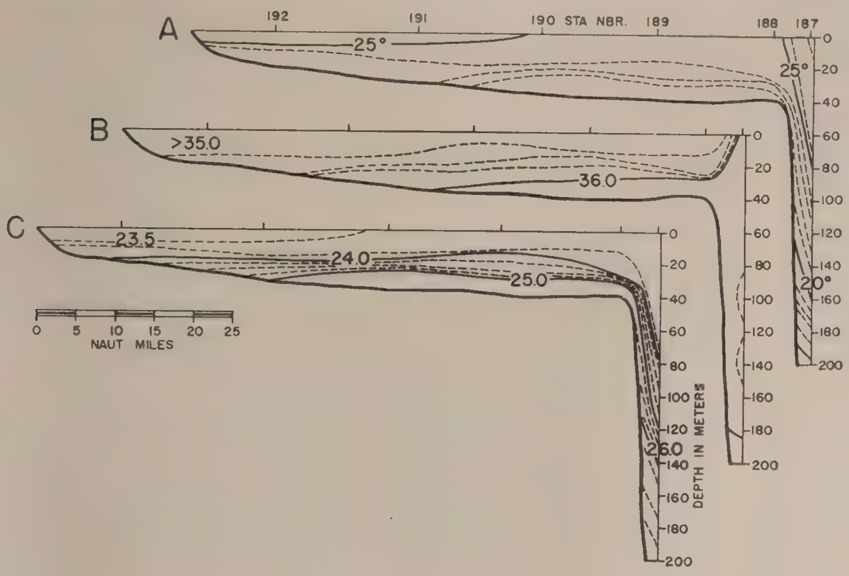

Fig. 5. (A) Distribution of temperature in ° C, (B) salinity in °/₀₀ and (C) density (σ_t), in Section IV, Onslow Bay, June 1953.

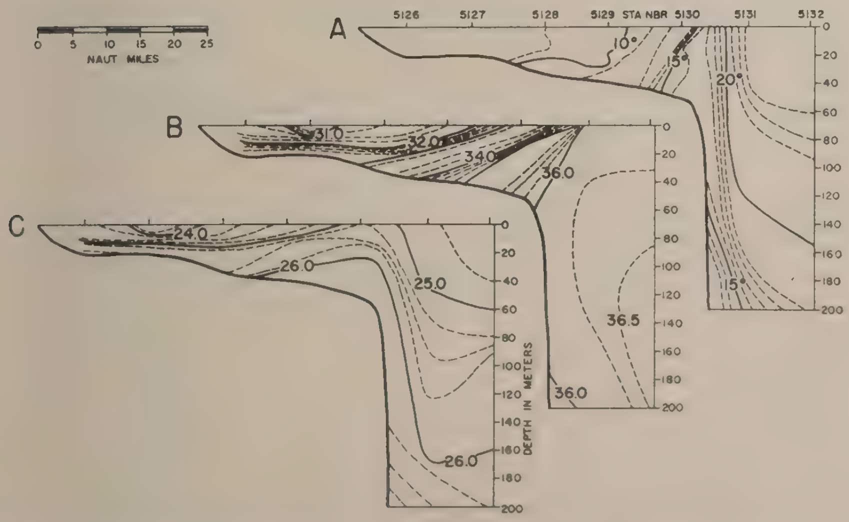

Fig. 6. (A) Distribution of temperature in C, (B) salinity in and (C) density (σ_t), in Section V, Wimble Shoals, January 1954.

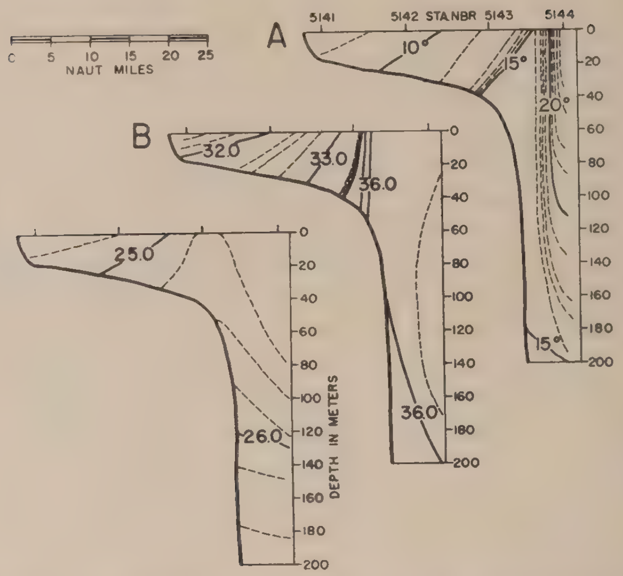

Fig. 7. (A) Distribution of temperature in ° C, (B) salinity in ‰ and (C) density (σ_t), in Section VI, Raleigh Bay, January 1954.

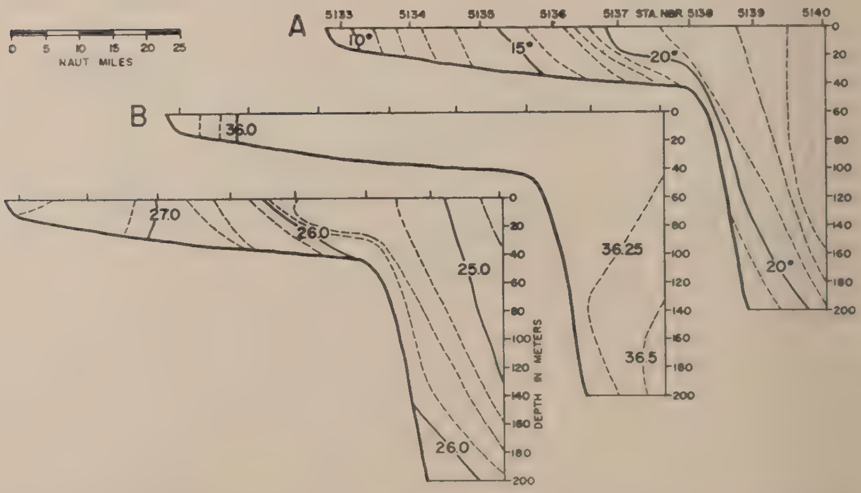

Fig. 8. (A) Distribution of temperature in C, (B) salinity in and (C) density (σ_t) in Section VII, Onslow Bay, January 1954.

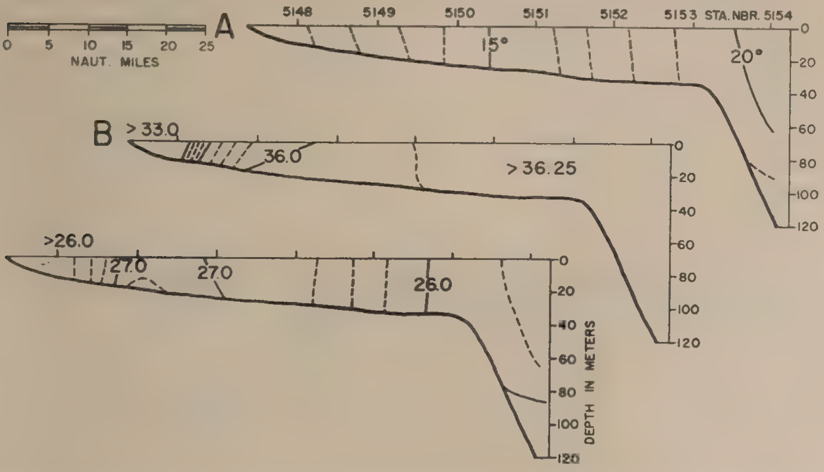

Fig. 9. (A) Distribution of temperature in ° C, (B) salinity in ‰ and (C) density (σ_t), in Section VIII, Long Bay, January 1954.

along the continental slope. During other parts of *Caryn* Cruise 64, the position of maximum current was observed to shift as much as 14 miles either side of the mean axis of flow (which off Onslow Bay normally lies about 18 miles south-east of the 100 fathom line. Associated with these shifts of position were onshore and offshore deflections in the direction of the current (von Arx, Bumpus and Richardson, 1955). This provides the energy to push water up the slope across the shelf. It also appears from salinity measurements that as the meanders move offshore they draw low salinity water (from the surface over the shelf) into the current.

The proximity of the Florida Current to the continental shelf precludes the occurrence (between the Current and the Carolinian coastal water) of slope water such as is found north-east of Cape Hatteras between the continental shelf and the Gulf Stream.

DISTRIBUTION OF THE CHAETOGNATHS

The chaetognaths collected in this area include 12 species representing three genera: *Sagitta bipunctata*, *S. enflata*, *S. helenae*, *S. hexaptera*, *S. hispida*, *S. lyra*, *S. minima*, *S. serratodentata*, *S. tenuis*, *Krohnitta pacifica*, *K. subtilis*, and *Pterosagitta draco*.

The quantitative composition of the plankton tows is recorded (Tables I and II). The species are listed in the order of their association with water of low or high salinity from left to right. The stations are arranged in the order of distance from the coast. The ranges of individual species overlap others considerably and in many cases completely. Nevertheless the tables show that there is a general correlation between salinity tolerance and the distance from the coast at which various species were found.

The most euryhaline–eurythermal species was *S. enflata* (Pierce, 1953), although it is doubtful if it can tolerate for long periods salinities as low as those in which *S. hispida* are usually found. *S. hispida*, *S. helenae*, and *S. tenuis* are species which are largely restricted to water of the continental shelf below Hatteras. The remainder of

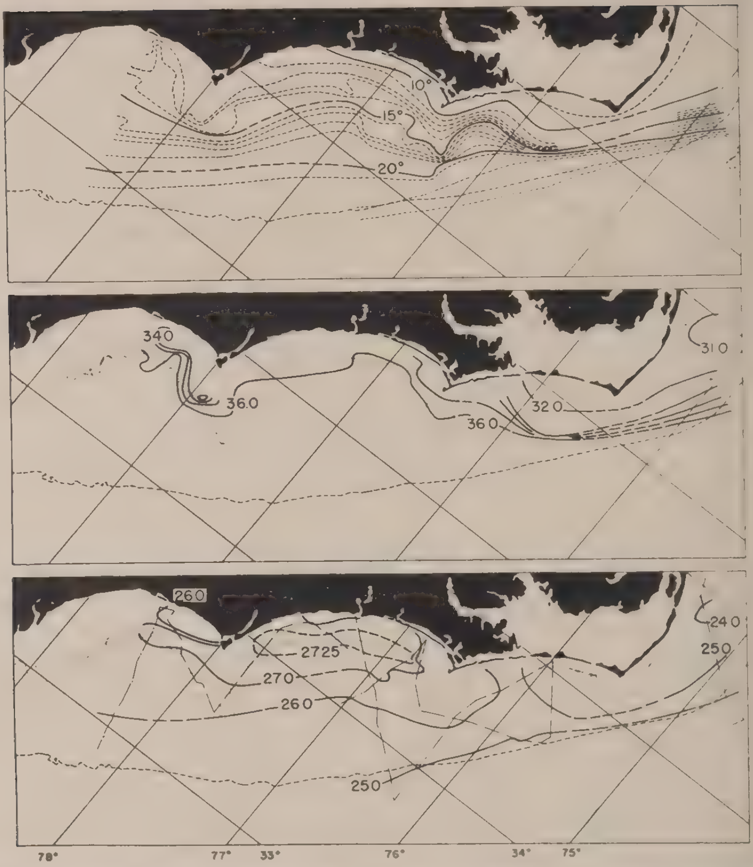

Fig. 10. Distribution of surface temperature in ° C (upper), salinity in ‰ (middle) and density (σ_t) (lower) on North Carolina Shelf, January 1954. Dash-dot line indicates track of ship.

the species were found principally in the Florida Current. The increase in number of species is evident as one proceeds offshore over the shelf into Florida Current water.

Sagitta bipunctata. The distribution and abundance of this species was similar in the area covered by spring (*Caryn* 64) and winter (*Atlantis* 196) cruises. *S. bipunctata* was collected in small numbers at several of the stations beyond the continental shelf and in a few instances they ranged shoreward about midway over the shelf (Tables I and II). With one exception (Station 5143) it was taken only in water where salinity was greater than 35·5 ‰. It therefore appears to be restricted in this region to Florida Current water or water recently mixed with such water. BIGELOW and SEARS (1939) did not find this species between Cape Cod and Chesapeake Bay.

Sagitta enflata was taken in almost every plankton sample on both cruises (Fig. 12). It was the most abundant chaetognath as well as the most widely distributed. The greatest concentrations were found near the edge of the shelf where as many as 160 per ten cubic metres were recorded. That they are sensitive to extreme conditions which are occasionally encountered in this area is borne out by their absence in the winter cruise from the three inshore stations north of Cape Hatteras. Here in water of less than 10° C and 32 ‰ not a specimen was found. Moreover only one specimen was present at the two inshore stations south of Hatteras, where the water had been derived from Virginian Coastal water driven around the cape.

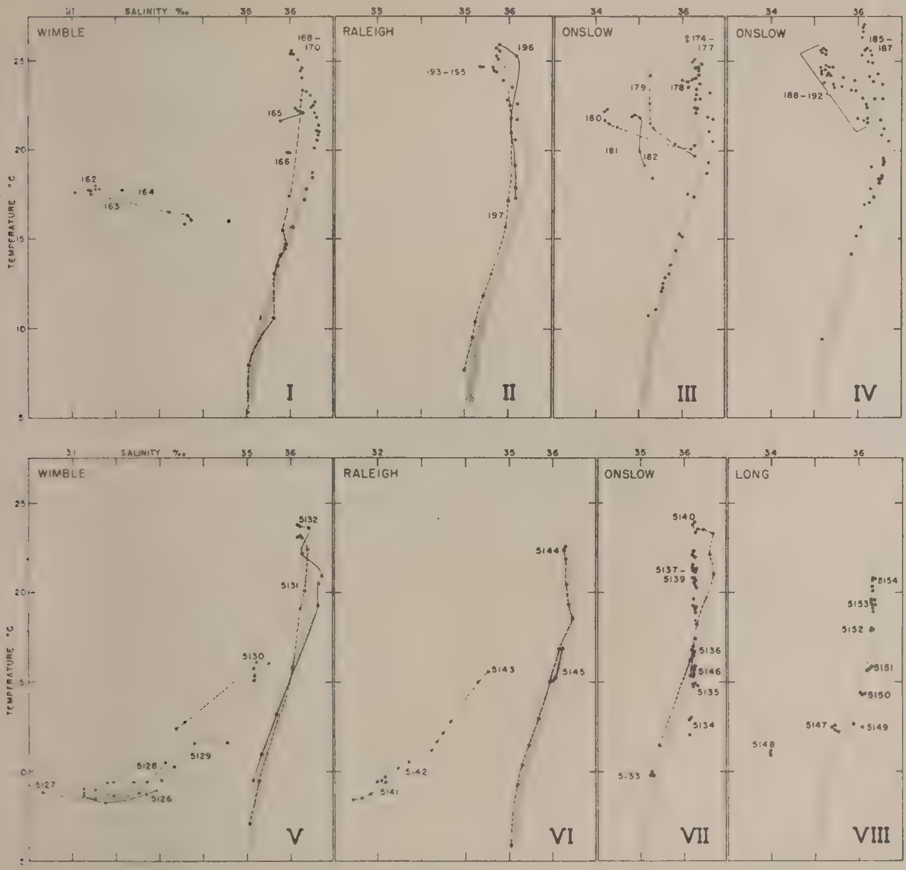

Fig. 11. Temperature–salinity diagrams, upper for *Caryn* Cruise 64, May and June 1953; lower for *Atlantis* Cruise 196, January 1954. The stippled line in the diagrams is the left side of an envelope describing the T–S characteristics of the Florida Current, PARR's (1937) stations in the Straits of Florida.

Sagitta helenae was found all over the continental shelf south of Cape Hatteras but it disappeared at the stations beyond the edge (Fig. 12). The greatest concentrations were found in the middle of the shelf where as many as 94 specimens per ten cubic metres were collected. This species is able to tolerate a rather wide range of salinity, varying from approximately 32 to 36 ‰. Although present in the edge of the Florida Current at times, it was never found far inside the current proper, and it does not appear from these data that it is a true inhabitant of such water.

This species has been closely associated with continental shelf water from the Gulf of Mexico (RITTER-ZAHONY, 1910; PIERCE, 1951, 1953) to Cape Hatteras. Apparently it disappears just north of the cape where the colder, less saline water is encountered over the shelf. Only a few specimens were taken near the edge of the shelf above Hatteras in the spring and winter cruises. BIGELOW and SEARS (1939) do not record this species in their plankton studies from Chesapeake Bay to Cape Cod. Because of its close relation to continental shelf waters from North Carolina southward, this species appears to be of special interest in its relation to the hydrography of this area. The movement of Virginian Coastal water around Hatteras in January displaced this species from the inshore stations in Raleigh Bay where it usually occurs (Fig. 12).

Table I

The distribution of chaetognaths by station during Caryn *Cruise* 64. *Species arranged in approximate series with respect to salinity, those which normally occur in coastal water on the left. Figures indicate number per* 10 *cubic metres of water strained*

Station No.	*Depth of Sample (metres)*	*S. enflata*	*S. hispida*	*S. tenuis*	*S. helenae*	*S. minima*	*S. serrato-dentata*	*S. bipunctata*	*S. hexaptera*	*S. lyra*	*K. pacifica*	*K. subtilis*	*P. draco*	*Total No. in sample*	*Volume strained (m^3)*
SECTION I—WIMBLE SHOALS															
165*	0·14	82				48	51						8	134	71
166	0·19	23				14	19	3	1	1				60	98
	0·40	111				6	44	3					3	120	72
SECTION II—RALEIGH BAY															
193	0·20	18		47	56									140	113
194	0·10	72		2	16									98	111
195	0·15	7		2	8		8	6			3		1	39	114
	15·30	83		3	79	11	5	1			1		1	163	89
196*	0·30	10						1			1			11	90
	30·60	38			4	35	4	1	1			3	1	244	270
197	0·80	46			2	8	18						3	100	131
	80·160					11	6			1		1		30	158
SECTION III—ONSLOW BAY															
182	0·12		9	1										7	73
181	0·20	4		5	27									84	152
180	0·15	35		1	10									65	141
	15·30	40		1	46									140	161
179	0·31	94		4	52	23								314	180
178	0·15	52		1	13		41				3			172	158
	15·30	54		2	32	10								164	168
177*	0·50	67			1	6	62				1	1	11	208	138
	50·100	29			1	29	5			1			2	184	287
176	0·30	4			2		54	2			2	2		110	163
	30·62	43			15	8	41						5	138	122
175	0·90	137			3	12	121	3			16			150	51
	90·180	11				3	7				2		1	31	122
174	0·80	30					39	4	2		3		18	198	206
	80·160	3				2	5	1	1			2	7	44	278
173	0·80	21				1	25		1			1	7	136	244
	80·160	1				1	4		1				1	17	300
172	0·75	3				1	5		4	1		1	1	24	207
	75·150	3				3	6		1			2	3	59	318
SECTION IV—ONSLOW BAY															
192	0·10													0	130
	10·20	2			5									11	140
191	0·13	54		1	25									65	81
	13·26	29		2	38	1								93	135
190	0·16	23			30		3							39	70
	16·37	23		41	70	20								98	98
189	0·20	102		6	10	16	2							114	84
	20·40	48		8	94	7								194	124
188*	0·20	35			4	1							2	35	83
	20·40	25			18	3	3						4	53	98
186	0·50	9					19						4	106	337
	50·100	1				1	1		2			1	1	23	385
185	0·65	30					24		2		2		3	184	297
	65·130					5	10		8			1	5	111	332
184	0·70	10					16		1		3		8	90	235
	80·140					5	6	1	1	1	1	1	2	60	297
183	0·80	9					19		2		1		7	89	231
	80·100	1				2	3		1	1	3	1		26	297

* One hundred fathom contour lies between this station and the next.

Table II

The distribution of chaetognaths by station during Atlantis *Cruise* 196. *Species arranged in approximate series with respect to salinity, those which normally occur in coastal water on the left. Figures indicate number per* 10 *cubic metres of water strained*

Station No.	*Depth of sample (metres)*	*S. enflata*	*S. hispida*	*S. tenuis*	*S. helenae*	*S. minima*	*S. serratodentata*	*S. bipunctata*	*S. hexaptera*	*K. pacifica*	*K. subtilis*	*P. draco*	*Total No. in sample*	*Volume strained (m^3)*
SECTION V—WIMBLE SHOALS														
5126	0·30			47									72	154
5127	0·20			21		2	1						34	141
5128	0·28			1		1							3	159
5129	0·45	1		7		1	19						47	167
5130*	0·25	34		5	2		45					2	145	165
5131	0·100	7											3	43
SECTION VI—RALEIGH BAY														
5141	0·15		1	98									113	115
5142	0·16			13		1	4						19	108
	12·24	1		8		1	8						29	169
5143	0·20	78		16	14	2	30			6		3	241	161
	20·40	49		15	4	2	10	1	2	1		2	152	178
5144	0·50	9		3	1	1	17	1	1			2	64	193
	50·100	8		3		1	21	1		1		4	79	208
5145	0·15	33		1	11	4	13	5		3		3	95	142
	15·30	2		1		1							5	120
5146	0·15	16		1	4	1	8			4		1	40	111
	15·30	11		3	7	1	4						26	97
SECTION VII—ONSLOW BAY														
5133	0·13	21	14	183	8								267	118
5134	0·19	59		30	66	7	2						401	185
5135	0·25	56		2	5	11	6			1		1	124	152
5136	0·28	3		2	2	2	2			1			14	120
5137	0·39	27		5	12	6	21			1		4	156	204
5138*	0·20	50		5	38		13			2		3	145	132
	20·40	9				1	3					1	22	147
5139	0·50	166		3	6	2	31	1		3		6	174	156
	50·100	25				6	23			3		3	78	129
5140	0·50	9					12	1	2		1	3	50	181
	50·100	6				4	6				1	5	40	192
SECTION VIII—LONG BAY														
5147	0·15	5 minute unidentified chaetognaths in sample											5	167
5149	0·15	83		10	68	3							97	59
5150	0·20	17		4	20	1							48	113
5151	0·24	13		3	50	2							89	133
5152	0·30	122		13	44	1	9			1		1	265	137
5153	5·30	89		1	22	1	5						198	168
5154	0·50	39			2	1	13			1		3	69	155
	50·100	29			1	1	5			1		1	84	226

* One hundred fathom contour lies between this station and the next.

Sagitta hispida is an inshore species which was taken at Stations 182, 5133, 5141 in water with a salinity of 31 to 35‰. No specimens were collected as far offshore as the ten-fathom line. Other records (PIERCE, 1951) indicate that this species is present in bays and at points close to shore south of Cape Hatteras.

Sagitta minima was taken many miles on either side of the continental slope (Fig. 12). It was not taken at the stations within the ten-fathom curve or at the stations farthest in the Florida Current.

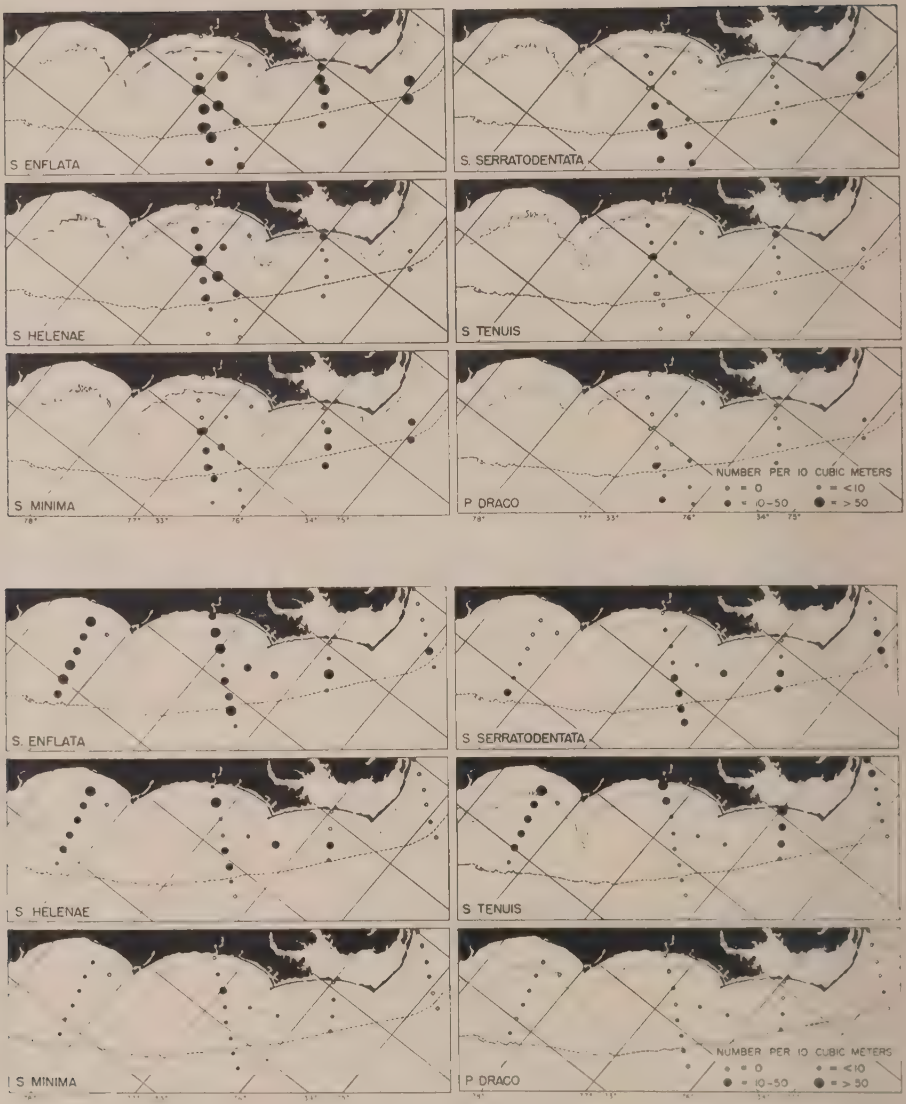
S ENFLATA
S. SERRATODENTATA
S HELENAE
S TENUIS
S MINIMA
P DRACO
NUMBER PER 10 CUBIC METERS
◦ = 0
• = <10
● = 10-50
⬤ = >50
78°
77°
33°
76°
34°
75°
S. ENFLATA
S SERRATODENTATA
S HELENAE
S TENUIS
S MINIMA
P DRACO
NUMBER PER 10 CUBIC METERS
◦ = 0
• = <10
● = 10-50
⬤ = >50

Fig. 12. Distribution of *S. enflata*, *S. helenae*, *S. minima*, *S. serratodentata*, *S. tenuis* and *P. draco*, upper in May and June 1953, *Caryn* Cruise 64, lower in January 1954, *Atlantis* Cruise 196.

It was a common chaetognath over the shelf but seldom appeared in numbers as large as *S. enflata*, *S. helenae*, or *S. serratodentata*. It was somewhat more abundant in the spring than in the winter and was usually associated with water close to 36°/₀₀ in salinity.

Sagitta serratodentata was one of the most abundant and widely distributed species found in these collections (Fig. 12). It covered the continental shelf in Carolinian and Virginian Coastal water from the ten-fathom line into the Florida Current as far as the stations extended. This species occurred commonly in numbers of 10 to 40 per ten cubic metres in both spring and winter and was noticeably more abundant near the edge of the continental shelf. Its distribution was similar to that of *S. minima* except that it was almost invariably more numerous in samples taken near the surface than in the deeper samples at any given station. This was true for samples taken during the day as well as at night.

Sagitta tenuis was restricted to the continental shelf waters both north and south of Cape Hatteras (Fig. 12). It extended from within a few miles of shore to the edge of the shelf. Many more specimens were caught and their range from shore was greater in the winter than in the spring. This species is one of the more euryhaline forms in this area, having been found in water ranging from less than 31 to 36·6$^{\circ}/_{00}$. It does not appear beyond the shelf where the Florida Current proper is encountered. Specimens were commonly found in greatest abundance at the less inshore stations. Like many other species in this area it was collected in water ranging in temperature from 9° to 25° C and little can be said about its optimum temperature.

Krohnitta pacifica and *K. subtilis* were never very abundant in any of the tows. They ranged from midway over the shelf outward as far as the stations extended. *K. subtilis* was noticeably rarer than *K. pacifica*. No significant difference could be seen between shallow and deep hauls in terms of either species or abundance. These species were almost always found in water whose salinity was 36$^{\circ}/_{00}$ or above. They were therefore directly associated with the Florida Current water. In the winter when a large incursion of Florida Current water moved into Onslow Bay a number of specimens of *K. pacifica* were taken in this water about as far inshore as it extended.

Pterosagitta draco was always identified in these catches with the warm saline water of the Florida Current (Fig. 12). Although one of the less abundant species it was widely distributed and found at almost all stations from midway over the shelf seaward. This species was closely associated with *K. pacifica* in these samples.

Sagitta hexaptera and *S. lyra* were also represented in some of the samples taken well inside the Florida Current. They were markedly more abundant in the spring than in the winter. Only a few *hexaptera* were found in the winter cruise and no *lyra*. Because they were present in small numbers their affinities are not obvious.

DISCUSSION

Chaetognaths were common and important members of the plankton community in all parts of the area studied. As a general rule those stations closest inshore and farthest offshore had fewer species than those near the edge of the shelf. The increase in number of species is the result of some of the typically shelf forms such as *S. tenuis* and *S. helenae* being present with species normally found in the Florida Current proper. This probably is the result of mixing which augments the total number of species in this area.

A comparison of the total number of chaetognaths collected at each station together with the abundance of each species shows surprisingly little difference between the spring and winter collections. The more abundant species such as *S. enflata* and *S. serratodentata* were abundant in spring as well as winter. *S. tenuis* was more abundant and widespread during the winter than in the spring. *S. hexaptera* was less numerous in winter, and *S. lyra*, an uncommon form in these collections was not found at all during the winter cruise.

Certain species of chaetognaths have been observed to exhibit diurnal vertical migration (Michael, 1911; Russell, 1933). In these cruises samples were taken at all hours. Position of the ship dictated when a sample would be taken rather than hour of the day or night. An inspection of these samples shows no consistent evidence for vertical migration or pronounced abundance of individuals in the shallow samples as compared with the deeper samples (Tables I and II). *S. minima* in the spring samples is an exception and does appear to be significantly more abundant in the deeper samples.

All species of chaetognaths collected in the area surveyed are known to occur in tropical and subtropical waters. None were typically Virginian (Table III). Published records do not show that *S. helenae*, *S. hispida* and *S. tenuis* are found over the continental shelf much farther north than Cape Hatteras. *S. minima* was found in the slope water over Block Canyon off Long Island in October 1952.* *S. serratodentata* in addition to being found in Florida Current, Carolinian and Virginian Coastal water, is found in Virginian and Boreal Slope waters (BIGELOW and SEARS, 1939; CLARKE, PIERCE and BUMPUS, 1943; REDFIELD and BEALE, 1940; HUNTSMAN, 1919).

Table III

*Distribution of chaetognaths with respect to water types**

Florida Current	*Carolinian*	*Virginian*
S. bipunctata		
S. enflata	S. enflata	
	S. helenae	
	S. hispida	
S. minima	S. minima	S. minima
S. serratodentata	S. serratodentata	S. serratodentata
	S. tenuis	S. tenuis
K. pacifica		
K. subtilis		
P. draco		
S. hexaptera		
S. lyra		

* No inference is made that these chaetognaths are indicators of the above water types, see text.

The Virginian Coastal water in the area just north of Cape Hatteras had relatively few chaetognaths present and none which could be selected as indicators of that water type. *S. elegans*, which occurs in abundance farther north in coastal water was observed by BIGELOW and SEARS (1939) to diminish in numbers in the offing of Chesapeake Bay. None were found in either of the Wimble Shoal sections in the present study. The higher temperature found in the southern portion of its range may be a limiting factor. COWLES (1930) reports it in Chesapeake Bay in salinities as low as 13‰.

The presence of a barrier to the southward movement of plankton in the Hatteras area is not as clearly demonstrated by the chaetognath distribution as one would expect in comparison with the hydrographic evidence. This is due to the lack of Virginian indicator species.† Evidence of the breaching of the barrier as far as Raleigh Bay in January 1954 is provided by the absence of the truly Carolinian species of chaetognaths, *Sagitta enflata* and *S. helenae*, at the inshore stations. Their distribution is compatible with the hydrographic evidence.

The occurrence and distribution of chaetognaths described in this study is in substantial agreement with the earlier investigation (PIERCE, 1953). PIERCE'S Zones I and II have been labelled Carolinian Coastal water. The difference between Zones I and II is a matter of dilution with river effluent. Zone III remains as unmodified Florida Current water. As was found to be the case in the earlier collections, the largest number of species was taken near the outer part of the continental shelf.

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* Personal communication from Dr. RICHARD BACKUS.

† The distribution of other elements of the plankton communities sampled in these collections is being examined by Philip St. John, a student at Harvard College.

The sources of Carolinian Coastal water are now better understood than heretofore. Mixing of Florida Current water with Carolinian Coastal water may be confined to the outer shelf zone or may occur over broad parts of the shelf. This is occasioned by the intrusion of the Florida Current up the slope along the bottom and across the shelf, penetrating more deeply into one bay than another. Occasional winter storm-driven indrafts of Virginian Coastal water may temporarily convert the inner part of Raleigh Bay from a warm, highly saline environment, to a cold, less saline one.

REFERENCES

Bigelow, H. B. (1933), Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. *Pap. Phys. Oceanogr. Meteor.*, **2** (4), 135 pp.

Bigelow, H. B. and Sears, M. (1935), Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. II. Salinity. *Pap. Phys. Oceanogr. Meteor.*, **4** (1), 94 pp.

Bigelow, H. B. and Sears, M. (1939), Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. *Mem. Mus. Comp. Zool., Harvard Coll.*, **54** (4), 183–378.

Bumpus, D. F. (1955), The circulation over the continental shelf south of Cape Hatteras. *Trans. Amer. Geophys. Un.*, **36** (4), (In press).

Clarke, G. L. and Bumpus, D. F. (1950), The plankton sampler—an instrument for quantitative plankton investigations. *Amer. Soc. Limn. Oceanogr., Spec. Pub.*, No. 5, 1–8.

Clarke, G. L., Pierce, E. L. and Bumpus, D. F. (1943), The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to the hydrographic conditions. *Biol. Bull.*, **85** (3), 201–226.

Cowles, R. F. (1930), A biological study of the offshore waters of Chesapeake Bay. *Bull. U.S. Bur. Fish.*, **46**, 277–381.

Fuglister, F. C. (1949), Average monthly sea surface temperatures of the Western North Atlantic Ocean. *Pap. Phys. Oceanogr. Meteor.*, **10** (2), 25 pp.

Huntsman, A. G. (1919), Biology of Atlantic water of Canada. Some quantitative and qualitative plankton studies of earlier Canadian plankton. III. A special study of Canadian chaetognaths, their distribution, etc., in the waters of the eastern coast. *Canad. Fish. Exped.*, 1914–15, *Dept. Naval Sci.*, 421–485.

Johnson, C. W. (1934), List of marine molluscs of the Atlantic coast from Labrador to Texas. *Proc. Boston Soc. Nat. Hist.*, **40** (1), 1–203.

Michael, E. L. (1911), Classification and vertical distribution of the chaetognaths of the San Diego region including some re-descriptions of some doubtful species of the group. *Univ. Calif. Pub. Zool.*, **8** (3), 21–86.

Miller, J. E. (1946), Cyclogenesis in the Atlantic coastal region of the United States. *J. Meteor.*, **3**, 31–44.

New York University (1954), Monthly frequencies of cyclogenesis in the east coastal region of the United States. In: Notes on cyclonic developments in the United States. *Tech. Pap.* No. 2, Project SCUD, College of Engineering, Research Division. (Unpublished manuscript).

Parr, A. E. (1933), A geographical-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. *Bull., Bingham Oceanogr. Coll.*, **4** (3), 1–90.

Parr, A. E. (1937), Report on hydrographic observations at a series of anchor stations across the Straits of Florida. *Bull., Bingham Oceanogr. Coll.*, **6** (3), 1–62.

Pearse, A. S. and Williams, L. G. (1951), The biota of the reefs off the Carolinas. *Elisha Mitchell Sci. Soc.*, **67**, 133–161.

Pierce, E. L. (1951), The chaetognaths of the west coast of Florida. *Biol. Bull.*, **100** (3), 206–228.

Pierce, E. L. (1953), The chaetognaths over the continental shelf of North Carolina with attention to their relation to the hydrography of the area. *J. Mar. Res.*, **12** (1), 75–92.

Redfield, A. C. and Beale, A. (1940), Factors determining the distribution of populations of chaetognaths in the Gulf of Maine. *Biol. Bull.*, **79**, 459–487.

Ritter-Zahony, R. von (1910), Westindische Chaetognathen. *Zool. Jb.*, Suppl. 11, **2**, 133–143.

Russell, F. S. (1933), On the biology of *Sagitta IV*. Observations on the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in the Plymouth area. *J. Mar. Biol. Assoc.*, U.K., N.S., **18** (2), 559–574.

Sutcliffe, W. H., Jr. (1950), Qualitative and quantitative study of zooplankton at Beaufort, North Carolina. *Thesis submitted to Duke University.*

von Arx, W. S., Bumpus, D. F. and Richardson, W. S. (1955), On the fine structure of the Gulf Stream front, *Deep-Sea Res.*, **3** (1), 46–65.

Williams, L. G. (1948), Seasonal alternation of marine floras at Cape Lookout, North Carolina. *Amer. Jour. Bot.*, **35** (10), 682–695.

Williams, L. G. (1949), Marine algal ecology at Cape Lookout, North Carolina. *Bull., Furman Univ.*, **31** (5), 1–21.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 110-114.

Experimental feeding of the copepod *Calanus finmarchicus* (Gunner) on phytoplankton cultures labelled with radioactive carbon (^{14}C)

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Summary—A small number of experiments were made on phytoplankton cultures labelled with ^{14}C; they confirmed earlier results obtained when using ^{32}P. With female *Calanus* the volume filtered varied from about 1–40 ml per day, and the digestion of a diatom and two flagellates lay between 50 and 80%.

Since both carbon and phosphorus are important constituents of the algal cell, it is fair to assume that the major part of the organic material is digested. It may be concluded therefore that, during a period of diatom abundance in the sea, most of the food ingested is utilized.

Qualitative work on the feeding of *Calanus* (Dakin, 1908; Esterly, 1916; Lebour, 1922; Marshall, 1924) has shown that it can ingest most of the small organisms present in the marine plankton, but that its diet consists predominantly of diatoms. It is possible that small naked flagellates are also important as food, but, since they have no indigestible skeleton, they can rarely be recognized in the gut, and not at all in the faecal pellets.

It has been possible to measure the quantity of different food organisms consumed by counting the numbers of these in a known volume of culture before and after a known period of feeding (Clarke and Gellis, 1935; Fuller and Clarke, 1936; Fuller, 1937; Clarke and Bonnet, 1939; Gauld, 1951). The earlier workers obtained values for the volume of water filtered of a few ml per day, but Gauld obtained an average of about 70 ml per day, using cultures of *Dunaliella* sp. (*Chlamydomonas*).

Recently some experiments have been carried out by Marshall and Orr (1955) on feeding *Calanus* with cultures of diatoms and flagellates labelled with radioactive phosphorus (^{32}P). These cultures were grown with a limiting quantity of phosphorus present, and were in most cases used after the phosphorus had been almost entirely taken up by the organisms. The initial concentration of ^{32}P in the culture was measured as well as that present at the end of the experiment in the body, faeces and eggs laid (if any). It was then possible to calculate the volume swept clear by the *Calanus* in 24 hours. This varied from less than 1 ml up to about 40 ml with a maximum in a single instance of a little over 80 ml.

The digestion of most of the food organisms was unexpectedly complete, the figures being usually over 60% and often over 90%. With a few organisms only was it apparently very low. It was high even when the *Calanus* were feeding rapidly in rich concentrations of food cells. These experiments show therefore that the phosphorus-containing portion of the algal cell is readily assimilated.

It seemed possible that the high digestion figures might be misleading, since various workers have shown that the phosphorus in algal cells is partly labile, and that this fraction may be either adsorbed on the cell surface or present in inorganic solution within the cell (Gest and Kamen, 1948; Kamen and Spiegelman, 1948; Goldberg, WALKER and WHISENAND, 1951; RICE, 1953). The error is not likely to be large, for RICE has shown that in cultures a week old with a low phosphorus concentration only about 2% is exchangeable. Most of our cultures were used when more than a week old, and when the phosphorus in solution had fallen to a low value.

It was, however, thought advisable to measure the digestion of some of the same organisms labelled with other radioactive isotopes. One of the most important elements in the plant cell is carbon, and by growing cultures using ^{14}C it was possible to measure the uptake and digestion in a way similar to that used with phosphorus.

There are certain disadvantages in the use of ^{14}C which are not met when using ^{32}P. Carbon is present in sea water as carbonate, bicarbonate and CO_2, and it is never limiting so that the plant cells cannot be expected to remove all the carbon present. The cells have therefore to be removed and re-suspended in non-radioactive water before use. Again carbon is liberated as CO_2 in respiration while the culture is growing, and also during the experiments, and although the value of this second figure may be small it will reduce the amount apparently used.

METHODS

The method adopted was in general similar to that used in the earlier experiments with radioactive phosphorus. The cultures were grown in sterile 250 ml conical flasks, to which were added 100 ml Erdschreiber culture medium and 50 ml of algal culture. The radioactive carbon was added in the form of bicarbonate, and 50 μc was found to be a convenient quantity for this volume of culture medium. The flasks were kept airtight by means of rubber stoppers to avoid possible loss of ^{14}C to the air as CO_2. The cultures were allowed to grow either in diffuse daylight or close to a fluorescent tube. They grew rapidly and well, and took up an unexpectedly high proportion (over 50%) of the added ^{14}C in a few days. For use in an experiment the culture was centrifuged at about 2500 r.p.m. for five minutes, the supernatant liquid decanted, membrane-filtered sea water added, and the organisms dispersed. This process was repeated twice more, and the cells finally suspended in membrane-filtered sea water in a dilution suitable for the experiment. For filtering the sea water a Gradocol membrane was used with an average pore diameter of about 0·9μ.

Since the β-radiation of ^{14}C is relatively weak and readily absorbed, it is necessary either to correct for absorption or to make all the samples tested strictly comparable.

The second procedure was adopted. The methods used are discussed by CALVIN, HEIDELBERGER, REID, TOLBERT and YANKWICH (1949). For sea water samples, uniform flat-bottomed dishes (planchettes) of 25 mm diameter were used. With a 0·2 ml delivery pipette the sample was put in the middle of the planchette and one drop of N/10 NaOH added. A circle of lens tissue of a diameter slightly less than the bottom of the planchette was then laid on the sample to spread the drop evenly so that, on drying, a layer of uniform thickness would be obtained. Drying was carried out on a hot plate. An attempt was made to increase the accuracy by using 0·5 ml instead of 0·2 ml, but it was unsuccessful because the self-absorption was relatively greater than with 0·2 ml, and the samples dried less uniformly.

The object of adding the NaOH was to avoid the exchange of CO_2 between the air and the bicarbonate of the sea water. If this procedure is not adopted, there may be a serious loss, and variable results will be obtained (CALVIN, *et al.*, p. 123). The lens tissue should not be silicone treated, since this type tends to curl up on drying. There was no tendency to curl with the photographic lens tissue used, so that the addition of collodion was unnecessary.

To ensure that no change in absorption of the radiation was caused by variations in salinity, the same sample of sea water was used throughout the experiments.

The activity of each sample was measured by exposing it in a holder at a constant distance from the mica end-window of a G.-M. counter, and the counts were recorded on a scaling unit. The results are expressed as counts per minute, but since we know the concentration of cells in the culture and the activity of both whole culture and filtrate, we can also express them as cell equivalents.

The bodies and faecal pellets of the *Calanus* have an appreciable self-absorption, and even after they had been torn up by needles the losses were considerable. Good duplicates were obtained by the use of a small disintegrator. This consisted of a narrow tube (diameter 9 mm) about 7 cm long, into which was fitted a perspex piston of almost the same diameter as the tube, and shaped at the foot to fit the bottom of the tube. The *Calanus* or the faecal pellets were put in the tube in about 0·5 ml of sea water, and the piston rotated by a small motor. By raising and lowering the tube the water and the *Calanus* or faecal pellets were forced past the rotating piston and thus disintegrated. After washing down the piston and tube and making the volume up to 3 ml, five aliquot samples were taken for measurement of activity. Microscopical examination showed that disintegration was almost complete. No fragments of a *Calanus* body could be recognized, and there were very few recognizable bits of faecal pellet. The disadvantage of the disintegration method is the dilution of the activity, since only 0·2 ml samples were used from the 3 ml of fluid. This can be countered by taking more sub-samples, or by making much longer counts.

In a feeding experiment a number of bottles of about 70 ml capacity were filled with the diluted culture prepared as described, and sampled for a count of cell number and activity. Into each bottle was introduced a single *Calanus*. Since females feed better than either Stage V or male *Calanus* they were always used. Each bottle was then tied in a black cloth bag (because *Calanus* feeds better in the dark than in the light), and attached to a wheel revolving about once every three minutes in a vertical plane. This keeps the culture cells from sinking to the bottom and so giving the *Calanus* an accumulation to feed on. Control bottles containing filtrate from the culture used were also set up to measure any uptake of ^{14}C from solution. Other control bottles, containing culture but no *Calanus*, were used to measure the ^{14}C returned to solution by the respiration of the plant cells.

After leaving them to feed for a suitable time, usually 15 to 18 hours, each *Calanus* was removed, washed three times to free it from radioactive water, disintegrated and sampled. The contents of the bottle were then poured into a flat-bottomed perspex dish with the inside angles bevelled, and the faecal pellets picked out under a binocular microscope. These too were washed, disintegrated, and sampled and their activity was measured.

The activity of the *Calanus* body added to that of the faecal pellets gives a measure of the total ^{14}C removed from the culture. From these and the culture reading can be calculated the number of cells ingested, the percentage digested and the volume of water swept clear. The results can be expressed either as counts per minute or as cell equivalents. The cell equivalent is a useful figure when considering the total amount taken up, but if we express the activity of the faecal pellets as cell equivalents, it must be remembered that each " cell equivalent " really represents several cells, the number varying according to the percentage digested.

EXPERIMENTAL WORK

Feeding experiments with female *Calanus* were made, using cultures of the diatom *Skeletonema costatum*, one of the more important spring diatoms in the sea, and the flagellates *Cryptomonas* sp. (Plymouth strain 23) and *Syracosphaera carterae*. The cultures when used were only a few days old, and were probably in the exponential growth phase. It was thought that some of the ^{14}C might be present in the inorganic form, either adsorbed on the cells or in solution inside. This was tested with *Skeletonema* by exposing samples on planchettes to the fumes of hydrochloric acid (STEEMANN NIELSEN, 1952), and comparing the activity before and after exposure. About 7% of the total disappeared with this treatment. With *Syracosphaera*, which possesses large numbers of calcareous coccoliths, the loss seemed to be greater but accurate measurements were not made.

The control bottle containing culture but no *Calanus* showed that, as a result of the respiration of the plant cells, the ^{14}C content of the filtrate had risen by 2–5%. This will cause a slight underestimate of the amount taken up by the *Calanus*.

A preliminary experiment was done with a culture of *Skeletonema costatum* in two different concentrations. It was thought that the activity of the faecal pellets and, in the lower concentrations, of the bodies also, would be too weak for the disintegration method, so they were torn up as finely as possible with needles and put in 0·2 ml of sea water on a planchette. Owing to self-absorption, this was not a satisfactory method, giving results which were too low, and it was therefore impossible to calculate the percentage digested. If we assume that this is the same as in a later experiment (see Table I), a figure can be obtained for the volume filtered which will be approximately correct for the richer concentration but minimal for the weaker. The estimated volume filtered in 24 hours in a concentration of 106,000 *Skeletonema* cells per ml varied from 1·6 to 4·0 ml in 24 hours, and in a concentration of 10,600 cells per ml from 5·7–42·5 ml. It is usual to find that in high concentrations of food cells filtration falls off, and the figures obtained compare well with our earlier experiments using ^{32}P.

Table I

Feeding experiments with Calanus using cultures grown with ^{14}C

Species	*Concentrations*	*Calanus* ♀	*Time of expt. in hours*	*Faecal pellets*		*Body less filtrate c/min*	*Total removed c/min*	*% used*	*ml filtered in 24 hr*
				No.	*Counts /min*				
Skeletonema costatum	1615 counts/ml/min	1	17½	54	278	817	1095	74·6	0·90
	144000 cells/ml	2	17½	17	192	283	475	59·6	0·38
Culture	0·01 counts/cell	3	17½	47	301	673	974	69·1	0·81
		4	17½	0	—	0	0	—	—
		5	17½	10	59	119	178	66·9	0·14
Filtrate	35 counts/ml/min	A	17½	4	36	38 } 43			
		B	17½	0	—	48			
Cryptomonas	1275 counts/ml/min	1	21½	38	170	585	755	77·5	0·66
	12600 cells/ml	2	21½	51	465	780	1245	62·7	1·10
Culture	0·10 counts/cell	3	21½	80	449	811	1260	64·4	1·13
		4	21½	56	220	454	674	67·4	0·58
		5	21½	57	516	589	1105	53·3	0·98
Filtrate	60 counts/ml/min	A	21½	2	—	0			
		B	21½	Lost	—	0			
Syracosphaera carterae	840 counts/ml/min	1	17	65	289	930	1219	76·3	2·07
	13500 cells/ml	2	17	38	86	180	266	67·7	0·45
Culture	0·06 counts/cell	3	17	45	392	885	1277	69·3	2·16
Filtrate	8 counts/ml/min	A	17	0	—	30			

The results of a second experiment with *Skeletonema* are shown in Table I. In this and subsequent experiments all the bodies and faecal pellets were disintegrated. As is usual in feeding experiments, individual variation was considerable; the number of faecal pellets varied from 10–54, and one *Calanus* did not feed at all. The amount digested varied from 60–75%, a figure very similar to that obtained with cultures labelled with ^{32}P. Unfortunately the *Calanus* were in poor condition and the volume filtered, less than 1 ml in 24 hours, was low. The activity of the culture was not high enough to give very accurate results. In both experiments with *Skeletonema*, the cell concentration was high compared with what is found in the sea.

In an experiment with *Cryptomonas*, which has cells about 20μ long, all the females fed well, although they filtered on an average only about 1 ml in 24 hours (Table I). The digestion ranged from 53–78%, as compared with 51–89% in cultures labelled with ^{32}P.

Finally, the experiment with *Syracosphaera* was carried out using three *Calanus* in a concentration of 13,500 cells ml. Judging by faecal pellet production, they fed well, but the maximum volume filtered was just over 2 ml in 24 hours (Table I). The digestion (68–76%), was decidedly lower than that found using *Syracosphaera* labelled with ^{32}P, in which it was usually over 90%. This may be due to the presence on its surface of a layer of coccoliths which would contain ^{14}C in the form of calcium carbonate.

The rate of production of faecal pellets was not high in any of the experiments with ^{14}C, the most rapid being found in a *Calanus* in *Skeletonema* culture, which produced an average of one every twelve minutes. It has been found that even with a much more rapid production, digestion of the phosphorus-containing fraction remains high.

ACKNOWLEDGEMENTS

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REFERENCES

CALVIN, M., HEIDELBERGER, C., REID, J. C., TOLBERT, E. M. and YANKWICH, P. F. (1949), Isotopic carbon. New York and London, 376 pp.

CLARKE, G. L. and BONNET, D. D. (1939), The influence of temperature on survival, growth and respiration of *Calanus finmarchicus*. *Biol. Bull.*, **76**, 371–383.

CLARKE, G. L. and GELLIS, S. S. (1935), The nutrition of copepods in relation to the food cycle of the sea. *Biol. Bull.*, **68**, 231–246.

DAKIN, W. J. (1908), Notes on the alimentary canal and food of the Copepoda. *Int. Rev. Hydrobiol.*, **1**, 772–782.

ESTERLY, C. O. (1916), The feeding habits and food of pelagic copepods and the question of nutrition by organic substances in solution in the water. *Univ. Calif. Publ., Zool.*, **16**, 171–184.

FULLER, J. L. (1937), Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. *Biol. Bull.*, **72**, 233–246.

FULLER, J. L. and CLARKE, G. L. (1936), Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull.*, **70**, 308–320.

GAULD, D. T. (1951), The grazing rate of planktonic copepods. *J. Mar. Biol. Assoc., U.K.*, **29**, 695–706.

GEST, H. and KAMEN, M. D. (1948), Studies on the phosphorus metabolism of green algae and purple bacteria in relation to photosynthesis. *J. Biol. Chem.*, **176**, 299–318.

GOLDBERG, E. D., WALKER, T. J. and WHISENAND, A. (1951), Phosphate utilization by diatoms. *Biol. Bull.*, **101**, 274–284.

KAMEN, M. D. and SPIEGELMAN, S. (1948), Studies on the phosphate metabolism of some unicellular organisms. *Symp. Quant. Biol., Cold Spring Harb.*, **13**, 151–163.

LEBOUR, M. V. (1922), The food of plankton organisms. *J. Mar. Biol. Assoc., U.K.*, **12**, 644–677.

MARSHALL, S. M. (1924), The food of *Calanus finmarchicus* during 1923. *J. Mar. Biol. Assoc., U.K.*, **13**, 473–479.

MARSHALL, S. M. and ORR, A. P. (1955), Studies on the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation and excretion in adult and Stage V *Calanus*. *J. Mar. Biol. Assoc., U.K.*, **34**, 495–529.

NIELSEN, E. STEEMANN (1952), The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J. du Cons.*, **18**, 117–140.

RICE, T. R. (1953), Phosphorus exchange in marine phytoplankton. *U.S. Fish and Wildlife Serv., Fish. Bull.*, **54** (80), 75–89.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 115-133.

The hydrography of the Gulf of Venezuela *

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and
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One of the very distinguished contributions of Henry B. Bigelow to the subject of oceanography is his study of the hydrography, plankton, and and fishes of the Gulf of Maine. It is the most complete description and analysis which exists of any circumscribed body of coastal water. Because of its breadth of outlook and high technical standard, this work is a model for studies in marine ecology. It is appropriate to contribute to this volume in Professor Bigelow's honour a sketch of the hydrographic conditions which are found in another gulf of somewhat similar proportions, but under far different influences than those which dominate the Gulf of Maine.

Summary—The distribution of salinity, temperature, oxygen, and total phosphorus in the Gulf of Venezuela is described.

The physical circulation appears to consist of two estuarine cells. The first is generated by the outflow from Lake Maracaibo, which terminates in a mixing zone over the sill off Calabozo Bay, where the water which occupies the deeper basin of the Bay is formed. The second is fed by water formed in this mixing zone which escapes seaward after mingling with more saline water drawn in from subsurface layers of the Caribbean.

The semi-diurnal components of the tide are augmented by resonance in the Gulf of Venezuela, and with the wind account for the vertical mixing which occurs over the sill of Calabozo Bay.

The trade winds, which predominate in winter, produce large seasonal differences in mean sea level across the Gulf, and control the distribution of the brackish water as it moves seaward from the outlet of Lake Maracaibo. Upwelling, which occurs in the lee of the Peninsula of Paraguana, is accompanied by an accumulation of phosphorus and a depletion of oxygen in the deep water near the coast. Similar conditions are found in the basin of Calabozo Bay.

The influence of countercurrents on the biochemical circulation is discussed.

The Gulf of Venezuela lies in the seaward extension of the syncline which forms the Maracaibo Basin. It opens directly on the deep water of the Caribbean Sea, and carries into it the entire outflow from Lake Maracaibo. This is the most substantial accession of fresh water along the Venezuelan coast of the Caribbean, and is estimated at 21 billion cubic metres per year. The northeast trades blow steadily along the axis of the Gulf from December through April. The annual range in temperature is small, being about 2° C at Maracaibo. Being situated in 12° N latitude the Corioli parameter is weak. Differences in salinity and the winds thus dominate the hydrography of the Gulf.

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* Contribution No. 776 of the Woods Hole Oceanographic Institution

The Gulf may be divided into two parts: the Outer Gulf and Calabozo Bay. These regions are separated by a sill with depths of 18 metres, extending along the 71st meridian. West of the sill a basin 28 metres in depth occupies the northern half of Calabozo Bay. East of the sill the bottom of the Outer Gulf slopes downward to provide depths of 40 to 80 metres over a considerable area. Access to the Gulf is probably limited to Caribbean water from depths not greater than 100 metres (Fig. 1).

The only earlier observations on the Gulf of which I am aware are measurements of surface salinities across the Gulf in December 1953 by GESSNER (1953 B, 1955), and a few records of chlorinity off the entrance to Lake Maracaibo by the Corps of Engineers, U.S. Army (1938). Undocumented statements relative to the water of Lake Maracaibo and its approaches, and on tide levels in the Gulf, are based on information secured by the Woods Hole Oceanographic Institution in the course of studies which it is expected to publish subsequently. These studies were made for the Creole Petroleum Corporation, which has graciously consented to the use of this information. The outflow of Lake Maracaibo was estimated from climatological data by DOUGLAS B. CARTER of the Johns Hopkins University Laboratory of Climatology (CARTER, 1954).

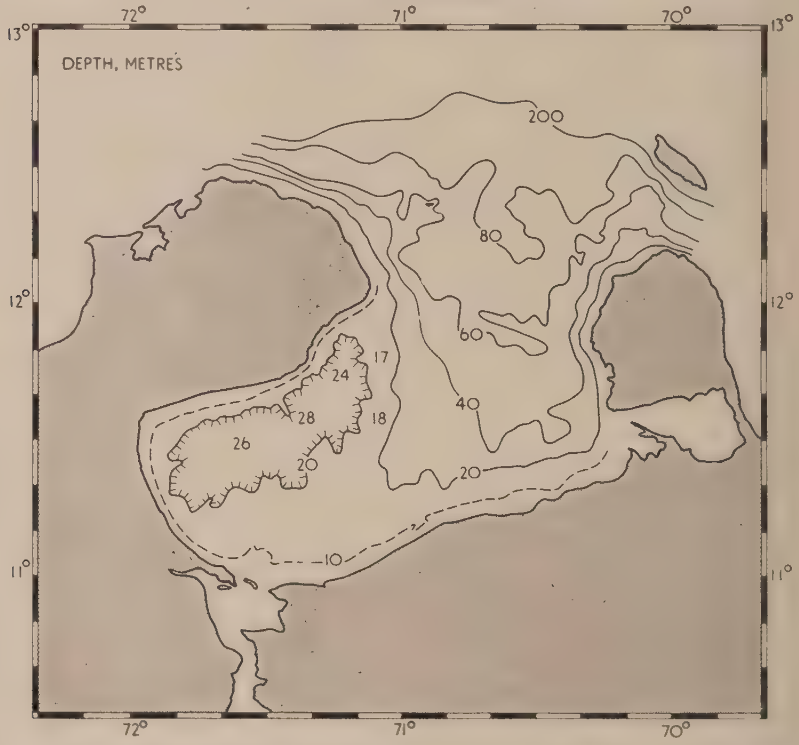

Fig. 1. Bathymetric chart of Gulf of Venezuela. Based on H.O. No. 5520—Depths in metres

The greater part of the data to be discussed was secured by the *Atlantis* between December 7 and 9, 1954. Three sections across the Gulf and two extending seaward from the adjacent capes provide information on the distribution of temperature, salinity, oxygen, and total phosphorus content (Fig. 2). I am greatly indebted to L. V. Worthington and W. G. Metcalf who secured this data and to Nathaniel Corwin who analyzed the samples for total phosphorus, using the method of Harvey (1948).

The data secured by the *Atlantis* are presented in Figs. 3 to 6, which show the distribution of the variables in the five sections occupied. Fig. 7 shows their distribution in a section along the axis of the Gulf.

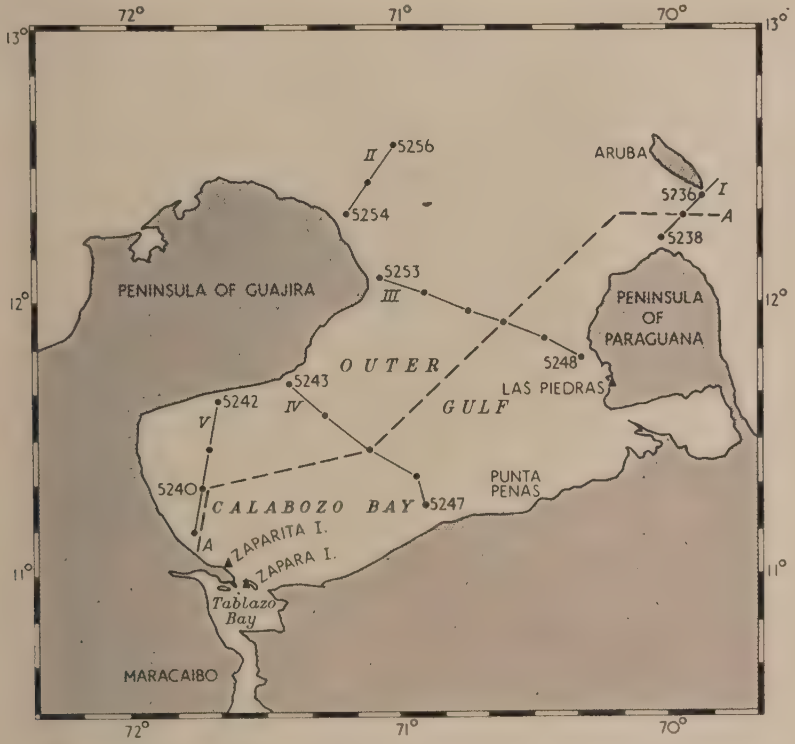
72°
71°
70°
13°
12°
11°
II
5256
5254
ARUBA
5236
I
A
5238
5253
III
PENINSULA OF GUAJIRA
PENINSULA OF PARAGUANA
5248
O U T E R
G U L F
LAS PIEDRAS
5243
5242
IV
V
5240
C A L A B O Z O B A Y
5247
PUNTA PENAS
A
ZAPARITA I.
ZAPARA I.
Tablazo Bay
MARACAIBO

Fig. 2. Position of hydrographic stations, sections and tide stations

THE PHYSICAL CIRCULATION

The Axial Circulation

The more general features of the circulation are shown by the distribution of properties along the axis of the Gulf (Fig. 7). The distribution of salinity is especially informative, since the fresh-water outflow from Lake Maracaibo serves as an indicator of the water movements.

In Calabozo Bay the circulation is estuarine. Along the western shore the outflow from the Lake produces a thin layer of brackish water of salinity less than 15‰. As this water moves seaward the salinity of the surface layer increases gradually to about 30‰ over the sill. A rather sharp halocline at about 15 metres separates the surface layer from water having salinities greater than 30‰ which occupies the deeper basin.

Over the sill, and on its seaward slope, there appears to be a zone of effective mixing, in which the surface water from the Bay mingles with the Caribbean water from the Outer Gulf. In this zone the salinity increases from 30 to >35°/₀₀ and does not vary greatly with depth. On one side this mixing zone produces the bottom water of

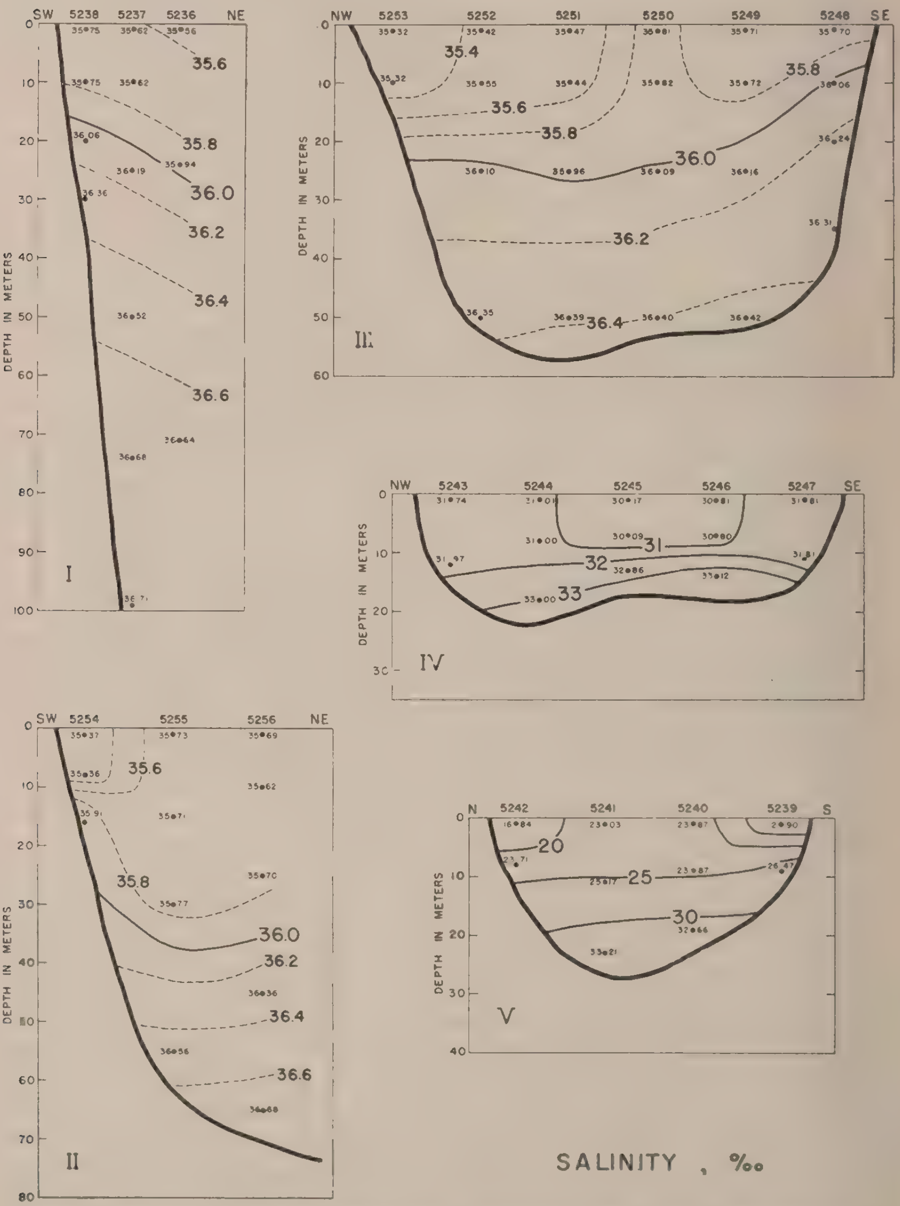

Fig. 3. Distribution of salinity in Sections I–V, Gulf of Venezuela. See Fig. 2 for positions

Calabozo Bay which, flowing westward as a countercurrent, supplies the salt consumed in diluting the outflow from the Lake. On the other side it produces a mixture so similar to the superficial layers of the Caribbean that its identity can be recognized only with difficulty.

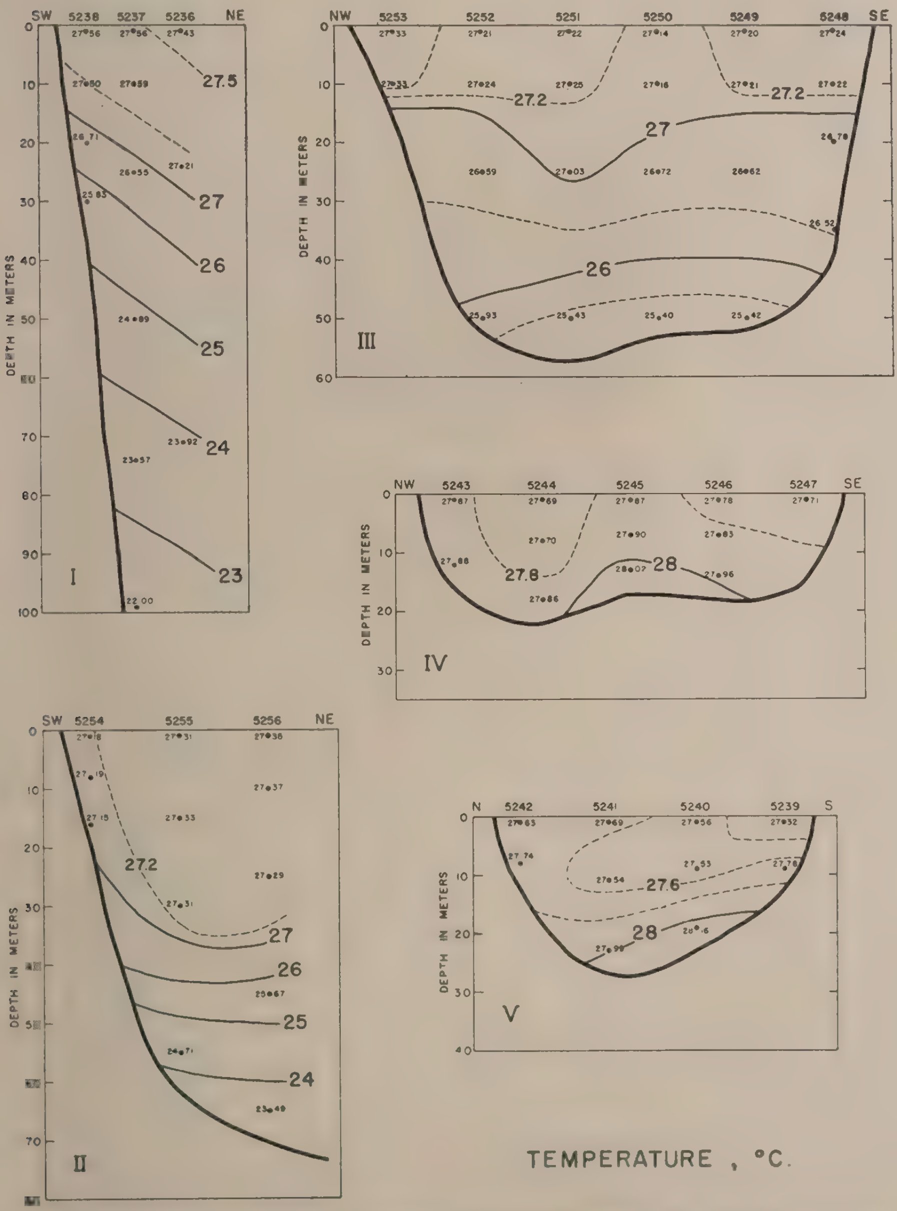

Fig. 4. Distribution of temperature in Sections I–V, Gulf of Venezuela. See Fig. 2 for positions

The distribution of temperature supports the above interpretation. The coolest surface water is found in the brackish outflow from the Lake. The surface water of Calabozo Bay warms as it moves toward the sill, where the warmest water and an almost uniform vertical distribution of temperature is found. The water of Calabozo

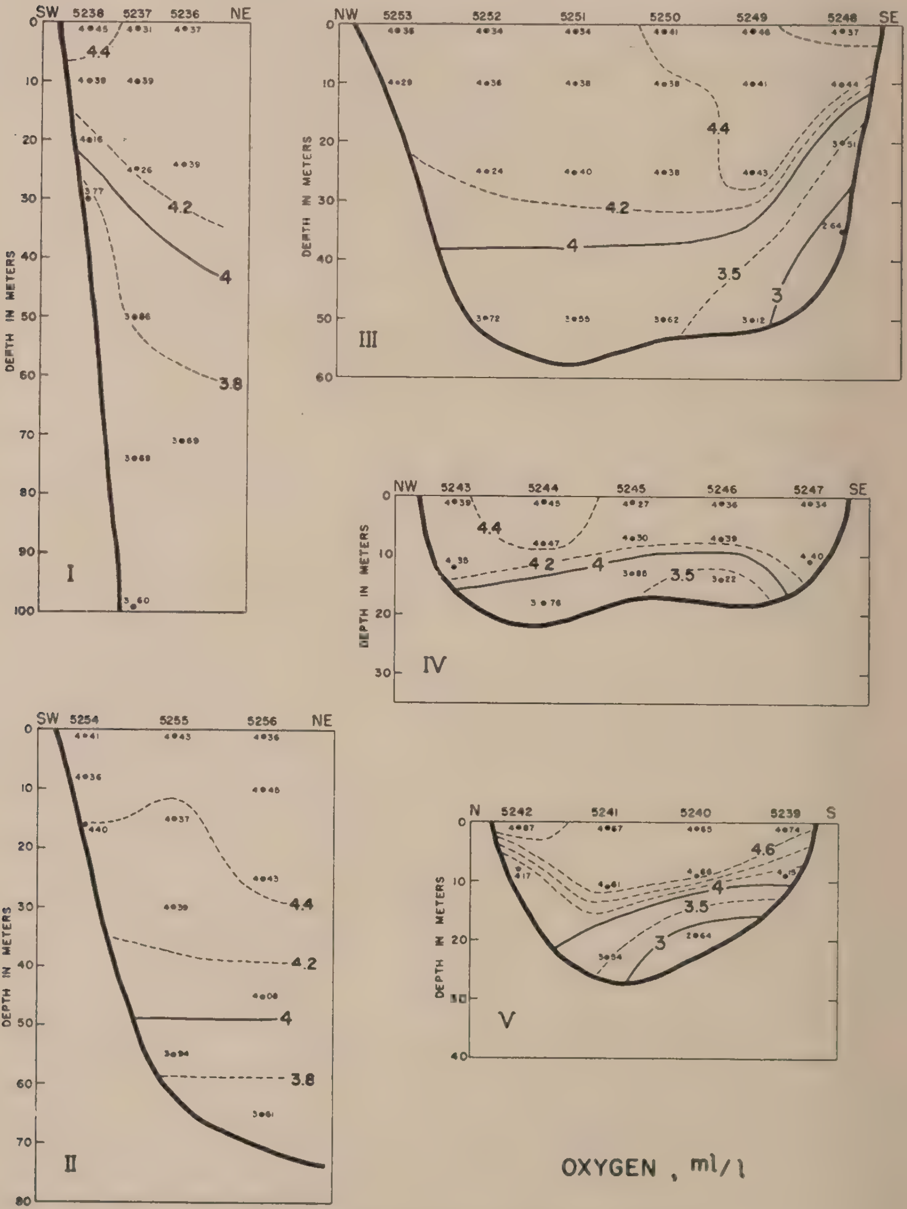

Fig. 5. Distribution of oxygen in Sections I–V, Gulf of Venezuela. See Fig. 2 for positions

Bay below the halocline is warmer (>28° C) than any other water in the region. This water cannot have arisen by direct advection from the deeper water of the Outer Gulf, which is colder and more saline.

Data from the files of the U.S. Hydrographic Office show that the mean monthly

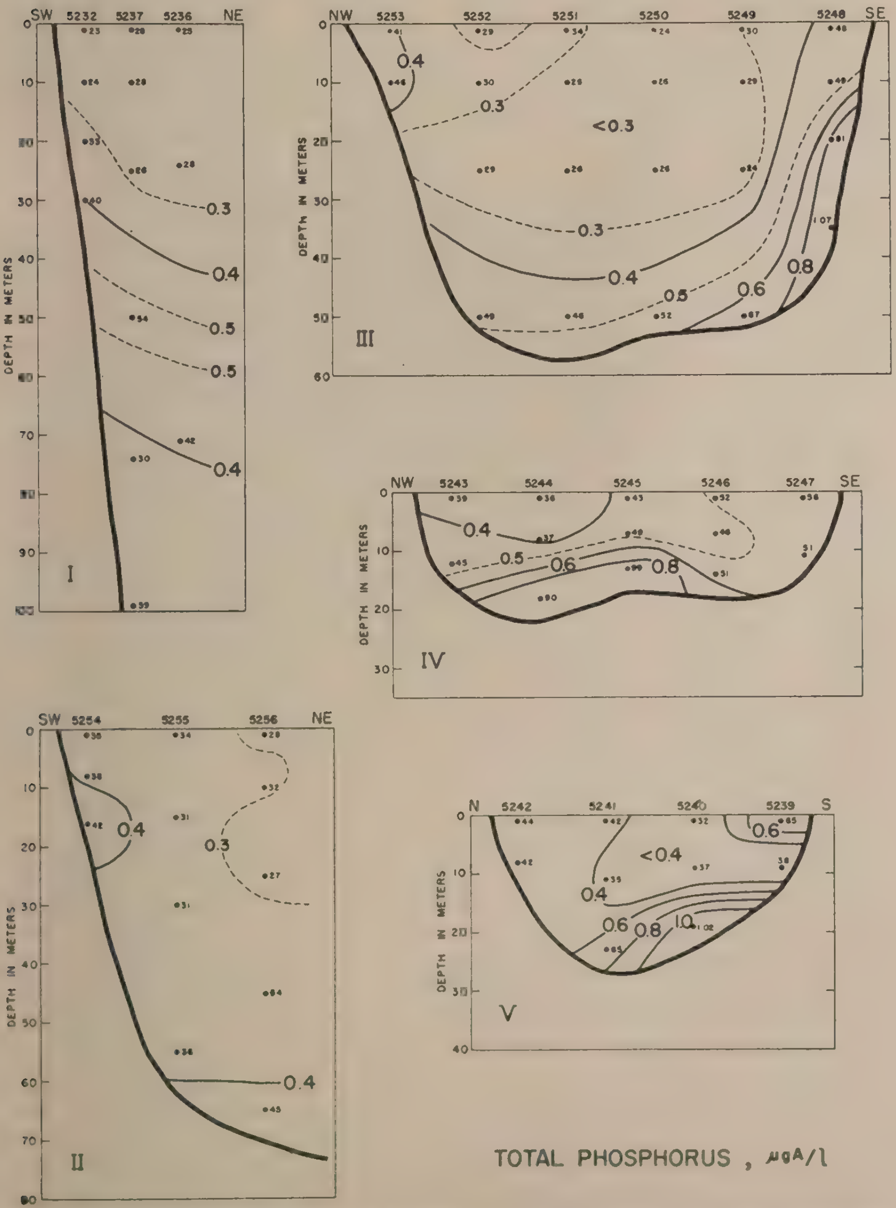

Fig. 6. Distribution of total phosphorus in Sections I–V, Gulf of Venezuela. See Fig. 2 for positions

temperature of the surface water of the Outer Gulf is at a maximum of 28·2° C in October, and falls to a minimum of 25·3° C in February. In December the mean value is 27·0° C, corresponding closely to the present observations. The high temperature of the deeper water of Calabozo Bay may be considered to have been acquired some months previously, when this water was formed in the mixing zone over the sill.

The distribution of phosphorus and oxygen also shows the stratification arising from the estuarine circulation of Calabozo Bay, the similarity of the water in the Outer Gulf to that in the Caribbean, and the independence of the deeper water of Calabozo Bay from that east of the sill. These properties are dependent on biological processes as well as on the physical circulation, and will be considered in more detail below.

The Horizontal Circulation

The distribution of properties in the several sections across the Gulf (Figs. 3–6) and in the surface diagrams (Figs. 8–11) shows no evidence that the brackish outflow from Lake Maracaibo is deflected to the right by the Corioli force, as is so frequently the case in the estuaries of higher latitudes. The water of low salinity formed at the outlet of Lake Maracaibo occupies a crescentic band along the western margin of Calabozo Bay (Fig. 8). The eastward extent of this band along the southern shore of the Gulf is not defined by the data. Along the northern shore it terminates abruptly in a convergence at 71° 30′ W. The Secchi disk showed an abrupt change in the transparency of the water across this convergence. This general distribution is reflected by the temperature and phosphorus content of the surface water.

Observations by the Corps of Engineers, U.S. Army (1938) show a northwesterly set of the alongshore currents off the outlet of the Lake, supporting the view that surface water is being transported at that point toward the western end of the Bay. The Sailing Directions for the West Indies (U.S. Navy Hydrographic Office, 1949) on the other hand state that a current, which sets south-westerly along the coast of the Peninsula of Guajira, turns eastward to flow along the southern coast of Calabozo Bay as far as Punta Penas (70° 30′ W), where it turns northward and is dissipated in the middle of the Gulf. A south-westerly set is described along the eastern shore of the Outer Gulf. This account indicates a convergence on the side of the Gulf opposite to that inferred from the *Atlantis* observations.

It seems probable that the north-east trade winds drive the brackish water formed at the outlet of Lake Maracaibo into the western end of the Bay, and tend to hold it against the shore. Escape is affected by alongshore currents, as discussed by LIVINGSTONE (1954). These currents appear to follow the coast of the Peninsula of Guajira until it turns northward, where they meet water moving into the Gulf along that shore, and both currents are deflected toward the middle of the Bay. Doubtless complex eddies exist throughout the Bay, but no pattern is revealed by the observations, nor any special path by which the fresh water works its way seaward. It may be that, as the trade winds slacken in summer, the brackish outflow from the Lake turns eastward under the Corioli influence, and sets up the pattern described in the Sailing Directions.

Although the water in the Outer Gulf resembles that in the Caribbean closely, small differences in temperature and salinity reveal the final steps in the escape of lake water to the Sea. Upwelling appears to occur along the Paraguana coast, as shown by the slope of the isohalines in Sections I and III, Fig. 3. This gives rise to a band of surface water having salinities higher than that found offshore, which extends north-

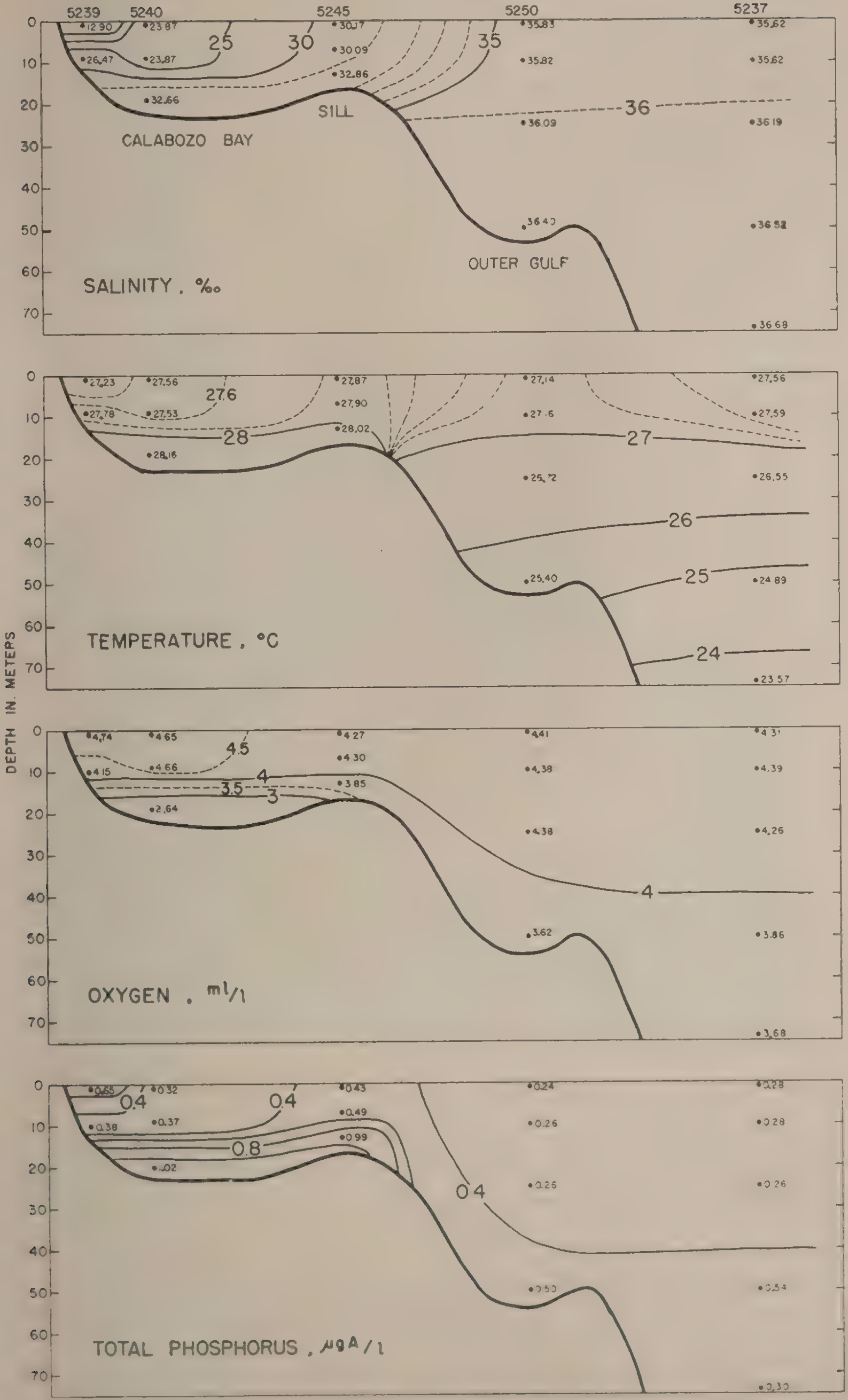

Fig. 7. Distribution of salinity, temperature, oxygen, and total phosphorus in Section A–A along axis of Gulf of Venezuela. See Fig. 2 for positions

westward from the Peninsula of Paraguana. It provides a component which, when mixed with water from Calabozo Bay, forms a mass of water slightly colder and less saline than the water of the Caribbean. This mass may be traced as it flows westwards close to shore around the Peninsula of Guajira (Fig. 8). The Sailing Directions report a westerly set of 1·75 knots off this headland during the greater part of the year.

In summary, the physical circulation of the Gulf of Venezuela appears to consist of two estuarine cells, separated by a transition zone of vertical mixing. The surface outflow of the inner cell is fed by water escaping from Lake Maracaibo, and is consumed in the mixing zone over the sill. This zone is the source of the deep countercurrent which provides salt to the surface outflow. The outer cell, less clearly defined, is fed by the water formed in the mixing zone, which escapes seaward at the surface after mingling with water from a countercurrent drawn in from the subsurface layers of the Caribbean. In both cells the surface drift is displaced to the left, under the influence of the wind.

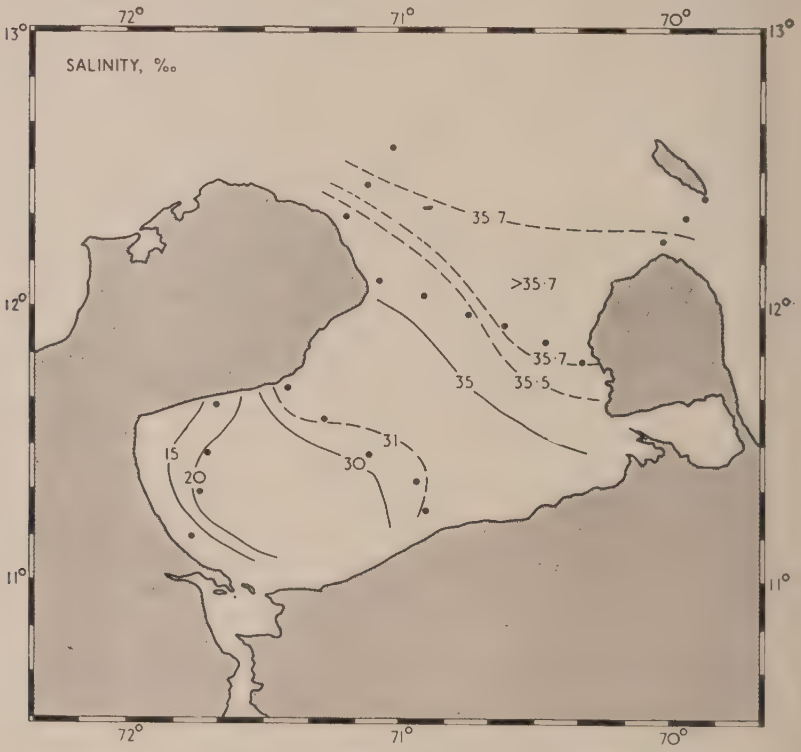

Fig. 8. Salinity at 1 metre depth in Gulf of Venezuela

The estuarine cell of Calabozo Bay finds its counterpart in many bays of the eastern coast of North America. Aside from the quantitative effects of the controlling topography, the more general difference in the circulation arises from the dominant effect of the prevailing wind on the horizontal flow in Calabozo Bay, as compared to the Corioli effect in the estuaries of higher latitudes.

Along the Atlantic coast the bays and estuaries discharge into, and lose their identity in producing, a broad band of coastal water of reduced salinity which separates the coast from the full sea water of the ocean. Along the Venezuelan shore a distinct band of coastal water is lacking, and Caribbean water in full strength penetrates the Gulf of Venezuela. The front separating the bay water from the full sea water is the mixing zone over the sill of Calabozo Bay. The water in this zone may be considered to be the rudimentary counterpart of the coastal water of the Atlantic coast.

If this view be accepted, the outer cell of the circulation of the Gulf of Venezuela finds its counterpart in those processes taking place along the margin of the Gulf Stream and in the slope water, by which the coastal water of the Atlantic coast becomes incorporated and lost in the general circulation of the ocean.

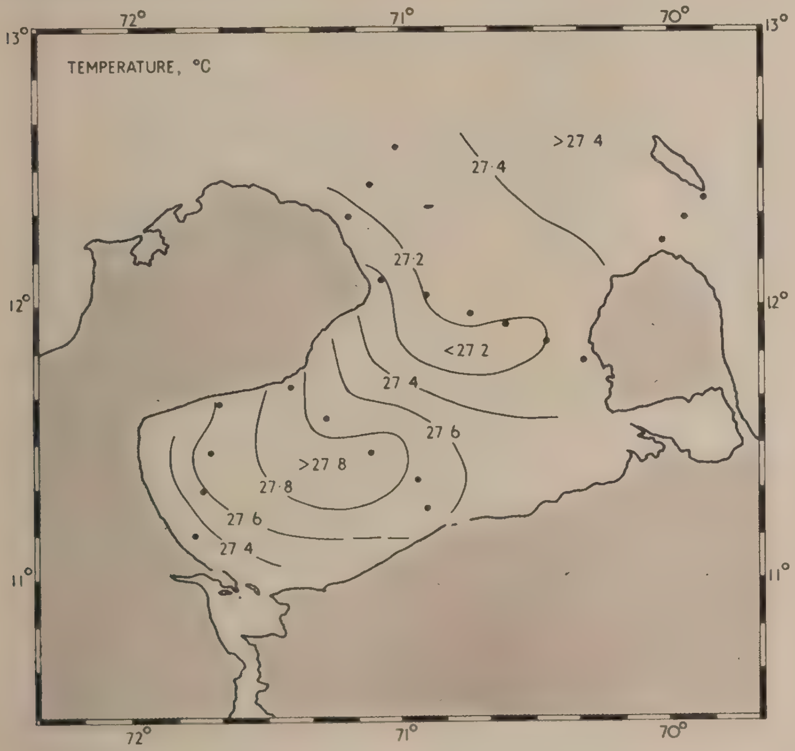

Fig. 9. Temperature at 1 metre depth in Gulf of Venezuela

Tides

The tides at Aruba, like those of the Caribbean in general, are of the mixed type in which the diurnal constituents predominate. The diurnal range of tide is 0·8 feet. In contrast, at Zaparita Island, off the mouth of Tablazo Bay, the tide is predominantly semi-diurnal and the mean range is 3 feet. The dimensions of the Gulf of Venezuela are such that the semi-diurnal constituents are augmented by resonance to a high degree, while the diurnal constituents are relatively unaltered.

A comparison of the harmonic contents of the tides (Table I) shows that the M_2 component at Aruba precedes that at Zapara Island by 123° or more than one-quarter period. High water occurs at Las Piedras only one-half hour earlier than at Zaparita Island, and 1·3 hours earlier than at Zapara Island. These relations place the antinode

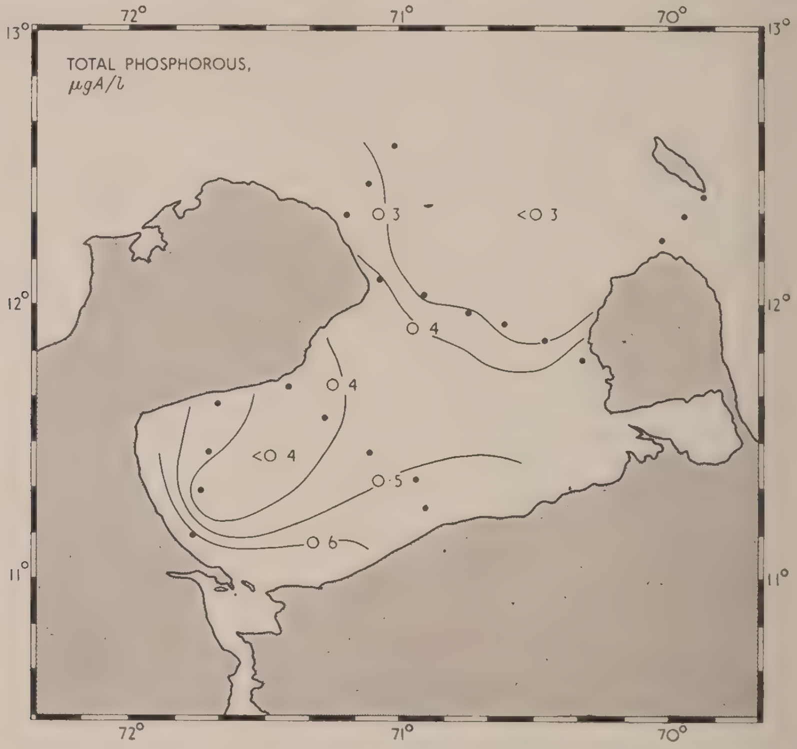

Fig. 10. Total phosphorus at 1 metre depth in Gulf of Venezuela

Table I
Tidal harmonic constants, U.S. Coast and Geodetic Survey (1951)

Constituent		*Greenwich Epoch* (*G*) *Aruba*	 *Zapara I*	*Amplitude* (*H*) *feet* *Aruba*	 *Zapara I*
Diurnal	K_1	241°	247°	0·3	0·24
	O_1	228°	246°	0·2	0·15
	P_1	241°	243°	0·1	0·08
	Q_1	—	244°	—	0·02
Semi-diurnal	M_2	161°	284°	0·13	1·04
	S_2	84°	217°	0·07	0·11
	N_2	282°	248°	0·03	0·32
	K_2	—	268°	—	0·03
Sum—Diurnal amplitudes				0·6	0·49
Semi-diurnal amplitudes				0·23	1·50
Ratio of sums				2·7	0·33

for the semi-diurnal tides across the entrance to the Gulf at a longitude intermediate between Aruba and Las Piedras. The amplitude of the M_2 component is increased eightfold, and the sums of the semi-diurnal components sixfold as the result of the resonance.

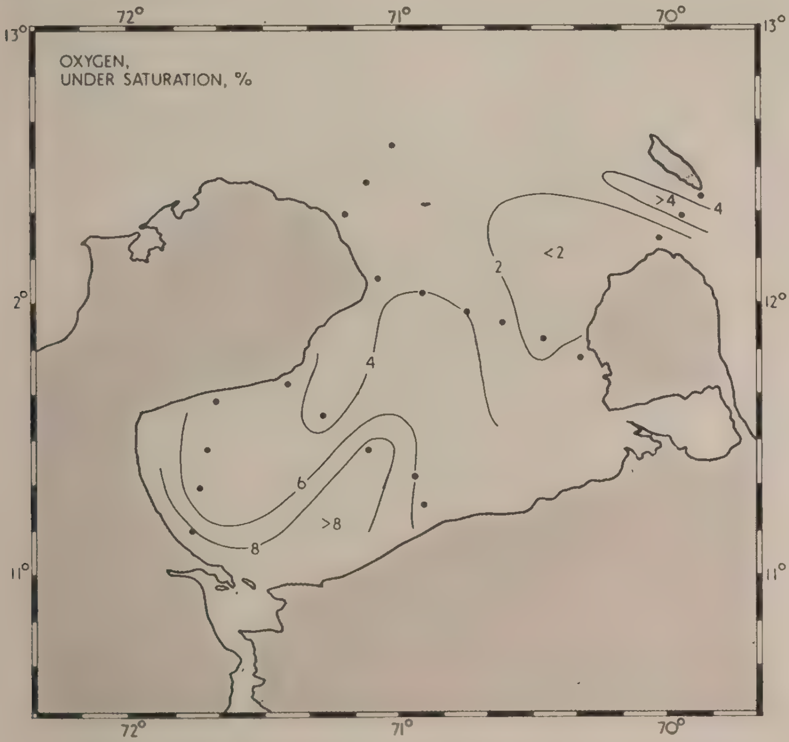

Fig. 11. Oxygen under saturation at 1 metre depth in Gulf of Venezuela

Since enough water must cross the sill of Calabozo Bay, having a depth of 18 metres, to raise and lower the level of the Bay nearly one metre twice daily, it is evident that strong tidal currents are to be expected over the sill. These currents, combined with the wind, account for the mixing which appears to occur in this region.

Water Levels

The monthly mean tide levels at Las Piedras change by as much as 0·8 feet in the course of the year (Fig. 12, A). The pattern is similar to that observed at positions on the Atlantic coast south of Chesapeake Bay and in the Gulf of Mexico (MARMER, 1951), and evidently is part of widespread phenomena. The monthly mean tide levels at Zaparita Island follow a similar pattern, but the annual variation in level is only 0·4 feet.

The mean annual difference in water level across the Gulf of Venezuela, between Las Piedras and Zaparita Island, is 0·92 feet in a distance of 93 nautical miles. The difference in level varies with the season, being highest (1·1 ft.) in January, and lowest (0·6 ft.) in October (Fig. 12, B).

The seasonal difference in levels across the Gulf is clearly related to the prevalence of north-easterly winds, as shown by wind data from Maracaibo (Fig. 12, D). The difference in levels may be explained in part by the reduced density of the water at the head of the Gulf. The magnitude of the difference is, however, so great as to raise a question as to the precision of the levelling between Las Piedras and Zaparita Island. There can be little doubt, however, that the mean tide level at Zaparita is one-half foot greater, relative to the level at Las Piedras when the north-east trades are at a maximum, than it is when their influence is reduced. Clearly winds which affect the slope of the sea surface so greatly are adequate to produce the effects on the circulation which have been deduced from the hydrographic observations.

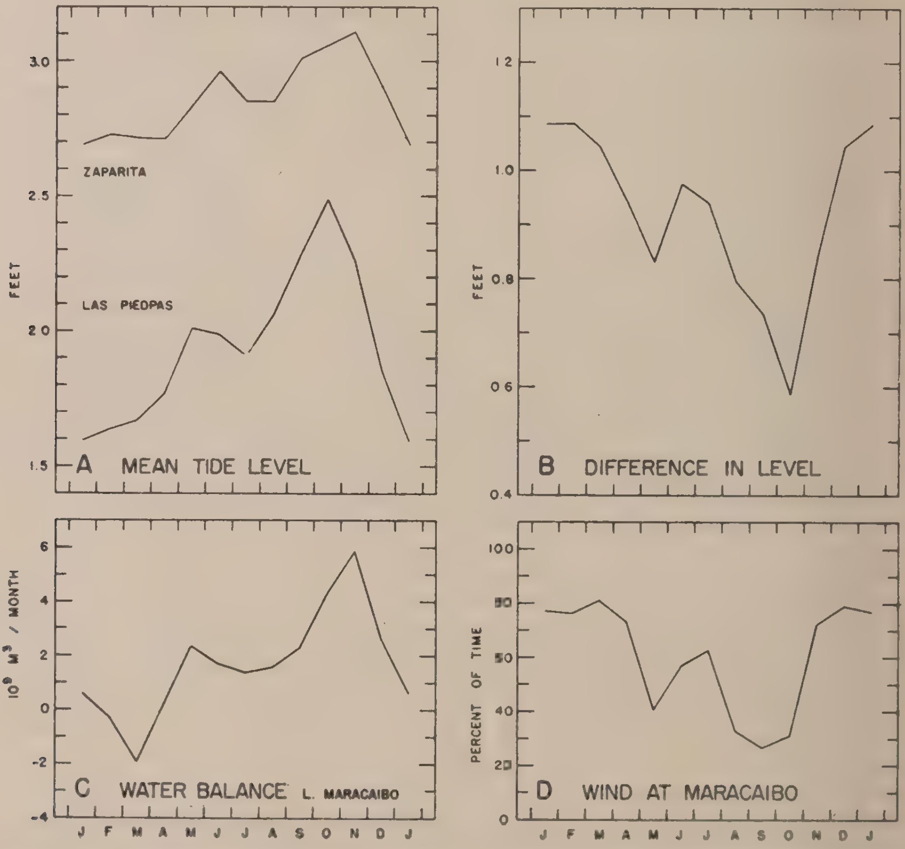

Fig. 12. *A*. Monthly mean tide levels. Average at Las Piedras for 1942–49 and at Zaparita Island for 1940–53. Data from Bar Survey, Maracaibo

B. Difference in average monthly mean tide level at Las Piedras and Zaparita Island

C. Average monthly net water balance of Lake Maracaibo. Estimated by CARTER (1954)

D. Per cent of time wind blew from N through ENE at Maracaibo, 1952. Data from Bulletin Bimensureal, Servicio de Meteorologia y Communicaciones, Ministerio de la Defensa, Fuerzas aereas, Maracay

Seasonal Influences on the Hydrography

The available data on the waters of the Gulf were collected in December. While there is no information on the conditions at other seasons, the annual variation in the two factors which control the circulation is known, and may be used to indicate the direction, if not the degree, in which the pattern will change with the season.

The rainy season in the Maracaibo Basin extends from April to December. The observations were consequently made at a time when the quantity of fresh water in the Gulf is maximal. During the following four months the outflow from the Lake is reduced and may come to an end (Fig. 12, C). The salinity of Calabozo Bay may consequently be expected to increase, and the hydraulic forces which drive its estuarine circulation to weaken. These tendencies should be reversed beginning in April. A rough estimate indicates that the quantity of fresh water present in Calabozo Bay in December is equivalent to about two years' outflow from the Lake. It is probable consequently that in the four months of the dry season the change in the mean salinity will be limited.

The effect of the north-east trade winds in maintaining the anticyclonic circulation in Calabozo Bay should continue through the winter. With the reduction in outflow from the Lake, the continued wind-induced motion will mix the water, and reduce the vertical and horizontal differences in salinity.

After April the winds become more variable and slacken in intensity. As the summer progresses, increasing outflow from the Lake should restore the salinity stratification. With the weakened effect of wind, the brackish water should spread more diffusely across the Bay. Possibly the Corioli force overcomes the wind influence and causes the escaping water to follow the southern shore to the eastward in the latter part of summer.

THE BIOCHEMICAL CIRCULATION

The distribution of the major elements in sea water, which determine the salinity, is the result of purely physical processes of advection and mixing. It may be used, consequently, to trace the general circulation of the water. In contrast, the distribution of those elements which are present in limited quantity, and which enter into the composition of organisms, may be profoundly influenced by biological activity. In particular, elements such as phosphorus and nitrogen, which become incorporated into the substance of the phytoplankton growing in the surface layers of the sea, tend to be carried downwards by the sinking of organisms, and are liberated at depth by the ultimate oxidation of the organic matter. There is thus a circulation of elements of biochemical importance which is different from that of the water itself, and of its biologically inert components.

In the case of the Gulf of Venezuela, data on the total phosphorus and oxygen content are available for an examination of the biochemical circulation.

Total Phosphorus

The total phosphorus content of water includes the phosphorus present as inorganic phosphate ions, as organic compounds present in solution, and as components of suspended organisms.

The total phosphorus content of the Gulf is higher than that of the source waters from the Caribbean. This is due primarily to the high phosphorus content of the water from Lake Maracaibo, which is on the average about 1·4 μgA per litre, whereas the Caribbean water contains about one-quarter this amount. The general pattern of distribution of salinity and phosphorus in the surface waters (Figs. 8 and 10), and in the axial section (Fig. 7), are so similar as to suggest that both properties vary as the result of the system of circulation which mixes waters derived from the Lake and Sea.

In the deeper parts of Calabozo Bay and the eastern side of the Outer Gulf, concentrations of phosphorus occur which are too great to be accounted for by the physical circulation (Figs. 6 and 7). In the former case the high salinity excludes an origin from lake water; in the latter the high phosphorus content precludes Caribbean water as the source. It is concluded that organisms and particulate matter have sunk into these basins, carrying down from the surface layers the phosphorus which has accumulated at depth.

Oxygen

In the Gulf of Venezuela the surface water, as well as that at greater depths, was everywhere under-saturated, in amount varying from 1·4 to 9·6 per cent. Physically this implies that the oxygen pressure was positive across the surface, and that oxygen was diffusing downward into the water. This condition cannot be explained by the cooling and consequent under-saturation of the surface, as is the case in higher latitudes in winter (REDFIELD, 1948), because the annual range in temperature is too small. It must be attributed to biochemical effects, arising from the excess of respiration over photosynthesis in the water.

The consumption of oxygen by respiration, in excess of its production by photosynthesis, can only persist if there is available some external source of organic matter, as is the case in waters polluted by sewage. The undersaturation of the surface waters of the Gulf of Venezuela may be the result of the high organic content of the outflow from Lake Maracaibo. In the lake water two-thirds of the phosphorus (1 μgA/l) is present in organic form, and while in the Lake much of this is probably present in living organisms capable of photosynthesis. On introduction into the Gulf, however, these organisms, which are fresh water or brackish species (GESSNER, 1953 A), may be killed by the higher salinity, and thus contribute to the quantity of organic matter immediately available for oxidation.

In support of this suggestion are the observations that the greatest under-saturation of surface water occurs in the immediate offing of Tablazo Bay (Fig. 11), and that the water of that bay is generally under-saturated with oxygen.

In the deeper parts of Calabozo Bay and the eastern parts of the Outer Gulf, where the total phosphorus was found to be anomalously high, the oxygen concentration is reduced to less than 3 ml per litre. (Compare Figs. 5 and 6). The deficiency in oxygen increases with the phosphorus content, and is about that to be expected from the increase in phosphorus if it arises from the oxidation of planktonic material (see Fig. 13). It may be concluded that the deficiency of oxygen in the deeper parts of the Gulf is due to the accumulation of organic matter as the results of the sinking of organisms and particulate matter from the surface layers of water, and that the greater part of this material has undergone oxidation.

At no place was the deeper water found to be completely devoid of oxygen. The deep circulation appears to be sufficiently rapid to prevent the accumulation of enough organic matter to exhaust the oxygen dissolved in the water. In the Strait of Maracaibo the water is flushed out each season by escaping lake water, to be replaced again with more saline water when the outflow slackens in the dry season. The oxygen content of the deeper water of the Strait is reduced to values comparable to those in the Gulf in the course of two or three months. Thus it is needless to assume that much more time is required to produce the conditions observed in the deeper parts of the Gulf.

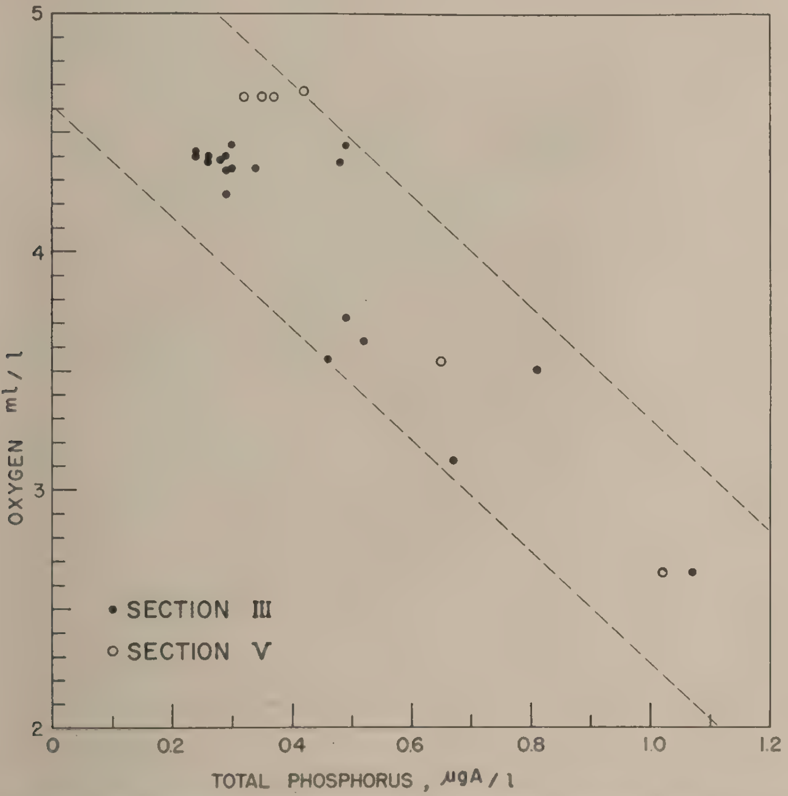

Fig. 13. Relation of oxygen and total phosphorus content of samples collected in Sections III and V. The slope of the envelopes is that required by the complete oxidation of organic matter from plankton of average composition; i.e., 2·35 ml O_2 is consumed in oxidizing organic matter containing 1 µ gA phosphorus

COUNTERCURRENT SYSTEMS AND BIOGENETIC PROPERTIES

The major ions of sea water exist in all parts of the ocean in very nearly equal proportions. It is a remarkable fact that, in contrast, most of those components which enter into the structure and chemical activity of living organisms are distributed in very different proportions in different parts of the oceans. Phosphate and nitrate, for example, are more than twice as abundant in the deep water of the Pacific and Indian Oceans than in the North Atlantic, although the concentrations of the major ions are approximately the same.

The concentrations of the organic derivative of sea water (phosphate, nitrate, and carbonate), and of oxygen, have been shown to vary from place to place in proportions related to the statistical composition of the plankton (REDFIELD, 1934). It is evident that some broad-scale process of biological origin is responsible for the distribution of these biogenetic properties in ways which are anomalous in respect to the purely physical character of the circulation.

The obvious mechanism for separating the organic derivative from the dissolved materials in one mass of sea water, and transferring it to another, is the sinking and subsequent decomposition of organisms into a deeper layer. Redistribution leading to accumulation or attenuation is then dependent on the horizontal movement of the respective layers. If such movements are consistently in opposite directions, great differences in concentrations may be developed. The counter-current principle is commonly employed in such physical mechanisms as heat exchangers. Its applications in physiology have been discussed by SCHOLANDER (1954).

The Gulf of Venezuela affords examples of two somewhat different types of counter-current system which lead to the local accumulation of phosphorus, with attendant depletion of oxygen in the deeper water.

In the Outer Gulf the winds appear to produce an offshore movement of the surface water, which is compensated for by an onshore counter-current at depth. This is referred to as upwelling. Organic matter sinking from the surface layer is carried landwards in the deep counter-current. The process leads to an attenuation of phosphorus content of the surface layer with distance from shore, and its augmentation in the deeper water which increases as the coast is approached. The degree of accumulation finally developed depends, of course, on a balance between this process and the dissipating effects of the circulation, which mixes the water vertically or transports it horizontally across the region of upwelling.

The situation in the Outer Gulf provides a small-scale example of the mechanism of enrichment of ocean water which occurs wherever trade winds give rise to upwelling along the continental coasts.

In Calabozo Bay the counter-current system of the estuarine circulation is engendered by the inflow of fresh water from Lake Maracaibo rather than by the wind. Otherwise the process leading to the attenuation of phosphorus in the surface water and its accumulation at depth is the same as in the upwelling system of the Outer Gulf. The degree of accumulation attained is limited by the rate of circulation of the deep water, which appears to move toward the head of the Bay, where it is most actively incorporated into the surface outflow. The highest phosphorus and lowest oxygen concentrations were found immediately off the outlet of the Lake.

The estuarine circulation of Calabozo Bay provides an example of a mechanism which must operate to varied degrees in many coastal embayments, fjords, and estuaries, and which may account in part for the greater fertility common to such enclosed waters, when compared to the off-lying sea.

REFERENCES

CARTER, DOUGLAS B. (1954), Report on water balance of the Maracaibo Basin. Unpublished manuscript on file, Woods Hole Oceanographic Institution.

Corps of Engineers, U.S. Army (1938), Model study of channel improvements at outer bar, Lake Maracaibo, Venezuela. *U.S. Waterways Experiment Station, Corps of Engineers, U.S. Army, Tech. Memo.* No. 106–1, 3 vols, December 1, 1938.

GESSNER, FRITZ (1953 A), Auf den Spuren Alexander von Humboldts in Venezuela. *Natur u. Wissenschaft*, 138 neue Zeitung, **20,** 13/14, Juni 1953.

GESSNER, FRITZ (1953 B), Investigaciones hidrograficas en el Lago de Maracaibo. *Acta Cientifica Venezolana*, **4** (5), 173–177, 4 figs., 4 tables.

GESSNER, FRITZ (1955), Die limnologischen Verhältnisse in den Seen und Flüssen von Venezuela. *Verhandl. Internat. Verein. für theoret. und angewandte Limnol.*, **12,** 284–295, 12 figs.

HARVEY, H. W. (1948), The estimation of phosphate and of total phosphorus in sea water. *J. Mar. Biol. Assoc., U.K.*, **27** (2), 337–359, 11 figs., 3 tables.

LIVINGSTONE, D. A. (1954), On the orientation of lake basins. *Amer. J. Sci.*, **252** (9), 547–554.

MARMER, H. A. (1951), Tidal datum planes. *U.S. Coast and Geodetic Survey, Spec. Pub.* 135,, 142 pp.

REDFIELD, ALFRED C. (1934), On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: *James Johnstone Memorial Volume*, Univ. Press, Liverpool, 176–192, 5 figs., 2 tables.

REDFIELD, ALFRED C. (1948), The exchange of oxygen across the sea surface. *J. Mar. Res.*, **7** (3), 347–361, 4 figs., 3 tables.

SCHOLANDER, P. F. (1954), Secretion of gases against high pressures in the swimbladder of deep-sea fishes. II. The rete mirabile. *Biol. Bull.*, **107** (2), 260–277, 5 figs., 4 tables.

U.S. Coast and Geodetic Survey (1951), *Tidal harmonic constants—Atlantic Ocean including Arctic and Antarctic Regions*, 137 pp.

U.S. Navy Hydrographic Office (1949), Sailing directions for West Indies, Vol. II, The Lesser Antilles and the coast of Venezuela. *H.O. Pub.* 129 (6th ed.), 335 pp.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 134-138.

The specific characters of the coral *Stylaster roseus*

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In the collections brought together by Dr. P. Wagenaar Hummelinck in the Leeward Islands and other parts of the West Indian region there are a few small colonies of a stylasterine coral with the following data: Curaçao, Plaja Djerimi, North corner, December 11, 1948 (rock, sand; tidal and lower zone). Examination of these corals showed that in all their salient characters they prove to correspond with *Stylaster roseus* (Pallas) as far as the eighteenth-century data on the species are concerned, while differing from the specimens identified with this name in recent literature.

The corals from Curaçao are four or five colonies of a more or less fan-shaped growth, occurring together on a fragment of dead coral rock. The colonies are up to 3 cm high and not over 3 cm broad. Each colony consists of a few stems of a breadth of about 5 mm, rapidly tapering upwards while giving off side branchlets which in their topmost parts have a thickness of about 1 mm. The stems and the thicker branches are slightly compressed in the flabellar plane of the colony. On the upper parts of the branchlets the cyclosystems occur alternately on the two lateral surfaces, whilst on the thicker branches the cyclosystems are distributed without apparent order; they are more numerous on the anterior than on the posterior surface. The number of dactylopores in the cyclosystems varies from 7 to 12; this number was counted in 100 cyclosystems with the following result: 5 cyclosystems with 7 dactylopores; 12 with 8; 28 with 9; 37 with 10; 14 with 11; 4 with 12; yielding an average of 9·55.

Except on the tops of the smaller branchlets the cyclosystems extend very little above the surface of the coral; their diameter varies from 0·5 to 0·7 mm. The gastropores have a depth of about 1 mm, and the gastrostyles have a length of 0·4 mm and a thickness of 0·15 mm, so that they are rather slender, occupying about one-third to one-half of the lower part of the gastropore (Fig. 1b). The gastrostyles are covered with small spines on the whole of their surface (Fig. 1a). Feebly developed dactylostyles (not drawn in Fig. 1b) are present in the dactylopores.

The colonies bear numerous ampullae of a hemispherical shape, scattered among the cyclosystems on the larger branches, or occurring in clusters densely covering large parts of the surface; as a rule the ampullae are numerous, especially on the posterior surface of the colonies. The ampullae have a smooth surface, without warts or spines, and their diameter varies from 0·6 to 0·8 mm, the size indicating that probably they are female ampullae.

The colour of the corals from Curaçao is yellowish with an irregular admixture of pink, occasionally turning to a light purplish tint in the topmost parts of some branchlets or on and around some cyclosystems on the larger branches.

Pallas (1766) gave a description of the coral named by him *Madrepora rosea*, mentioning some characters which at present still may be regarded as typical of the species; this description was based on an examination of specimens in Dutch collections. In Houttuyn's (1772) account of the coral, the salient data are mentioned as noted by Pallas; Houttuyn's work is here cited because it contains the first figure of the species (1772, Pl. 129, Fig. 4, copied in Fig. 2 of the present paper). This figure again appeared in a treatise by Müller (1775, Pl. 23, Fig. 4), which practically is a translation of Houttuyn's work with a few additional remarks. Esper (1794) gave an elaborate description of the species, based on a specimen from a German collection, his figures (1794, Madrep., Pl. 36) represent a coral of a shape similar to that of

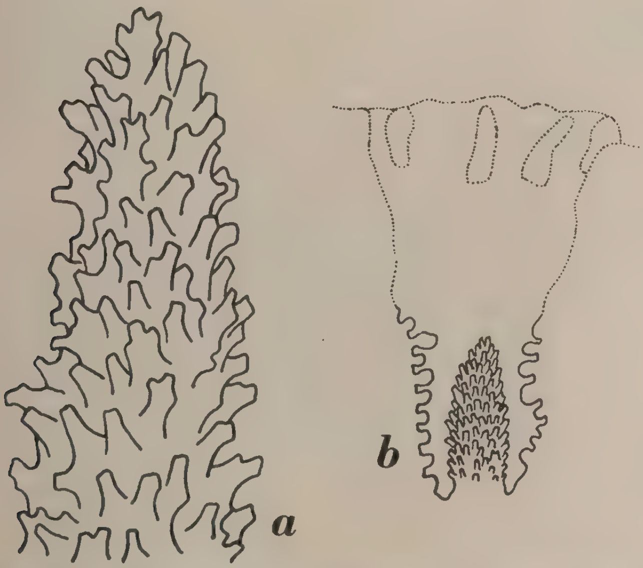

Fig. 1. *Stylaster roseus* (Pallas) from Curaçao. (a) gastrostyle, × 250; (b) longitudinal section of a cyclosystem, × 60

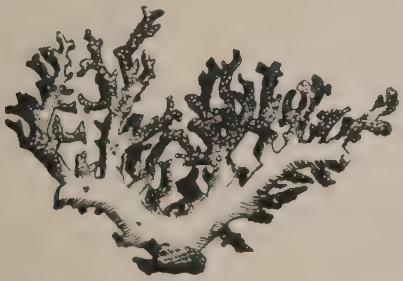

Fig. 2. Copy of the figure of *Madrepora rosea* Pallas in Houttuyn (1772, Pl. 129, Fig. 4). Original size

Houttuyn. The data noted here contain the original contributions towards a knowledge of the species; remarks in other eighteenth-century publications were copied from the cited works.

According to Pallas, the colonies of his *Madrepora rosea* are " semi-palmares " (half a hand high, about 5 cm); Esper records the height of large specimens as " zwey bis drey Zollen " (about 5 to 7½ cm). The two authors further state that the basal parts of the stems are comparatively thick, and that they gradually taper to very thin terminal branchlets while giving off numerous side branchlets. At that time the only known locality of occurrence of the species was " Mare circa Insulam St. Domingo " (Pallas), " an den Küsten der Insel Domingo " (Esper), the quoted passages referring to the eighteenth-century name of the island Haiti in the West Indies. It stands to reason that the corals which were collected nearly two hundred years ago came from shallow water.

It is interesting to note that the corals from Curaçao, on account of their small size and of their gradually tapering branches, closely correspond with the specimens described and figured by Pallas, Houttuyn, and Esper, thereby differing from the other species of *Stylaster* known to occur in the West Indian region, which attain a larger size and have branches of a much slenderer growth.

Lamarck (1816) placed the species *Madrepora roseus* in the genus *Oculina*; Gray (1831) erected the genus *Stylaster*, in which he placed the two species *Oculina rosea* and *O. flabelliformis*; in 1850 Milne Edwards and Haime (1850–1854) selected *Stylaster roseus* as the type of the genus *Stylaster*. In another paper (Milne Edwards and Haime, 1850) there is a rather elaborate description of *Stylaster roseus*, in which the authors state that they have never seen colonies of a larger size than a few centimetres, the thicker branches of which have a thickness at the base of 5 to 6 millimetres. These data correspond with those of the corals from Curaçao; in other details, however, there are slight differences: Milne Edwards and Haime remark that the number of dactylopores in the cyclosystems is from 10 to 14, most commonly 12, while the diameter of the cyclosystems is nearly 1 mm, these figures being somewhat higher than in the specimens from Curaçao. The measurements of the ampullae in the specimens of Milne Edwards and Haime (not over ½ millimetre) perhaps indicate that these were male ampullae.

Pourtales (1871, p. 83) remarks that *Stylaster roseus* is " abundant on the under surface of blocks of coral rock, on the reef at Cruz del Padre, north coast of Cuba, a couple of feet below low-water mark ". Moseley (1880, p. 79) refers to this occurrence of the species in almost the same words, and on another page (*loc. cit.*, p. 77) remarks that " ampullae are especially well developed in the shallow water *Stylaster roseus*; those in the female stocks being very large and prominent ".

A coral of rather common occurrence in depths of 120 to 324 fathoms (220 to 592 metres) off the Florida Reef was described by Pourtales (1868) as *Stylaster erubescens*; with some slight changes this description again appeared in a later paper (Pourtales, 1871); the following details are taken from the latter, the terminology partly being altered to a more modern wording: younger branchlets slender, with rather close-set alternate cyclosystems, these slightly prominent, 1·2 to 1·5 mm in diameter, deep; nine to twelve, most frequently eleven dactylopores in a cyclosystem; gastrostyle deeply sunk, rounded and hirsute; dimensions, height and breadth of flabellum, 10 cm. On Plate 4 of the cited work is figured a colony of *Stylaster erubescens* in natural size (Fig. 10), and the terminal part of a branch, 4 times enlarged (Fig. 11). The figures show that the tendency for a lateral arrangement of the cyclosystems on the branches is much more obvious than in the specimens from Curaçao, that the branches are much less pronouncedly tapering, and that the cyclosystems definitely extend over the surface of the branchlets, the smaller branchlets thereby becoming distinctly zigzag-shaped, in contradistinction to the corresponding parts of the specimens from Curaçao. The cyclosystems of *Stylaster erubescens* (diameter 1·2–1·5 mm) are about twice as wide as those of the specimens from Curaçao (diameter 0·5–0·7 mm), and distinctly wider than in the specimens of *Stylaster roseus* examined by MILNE EDWARDS and HAIME (diameter nearly 1 mm). The most important difference of the two forms is that of the entirely different shape of the gastrostyle, which in *Stylaster erubescens* is rounded (almost spherical), in the specimens from Curaçao conical, more than twice as high as broad (Fig. 1).

The Stylasteridae of the North Atlantic region remained imperfectly known till 1914, when BROCH'S important paper appeared dealing with the specific characters of *Pliobothrus symmetricus* Pourtalès, *Allopora norvegica* (Gunnerus), *Stylaster gemmascens* (Esper), and a species named by BROCH *Stylaster roseus* (Pallas). The material of the last named came from depths between 263 and 1,400 metres; BROCH notes that the colonies display a marked difference between small branches, main branches, and stem, that the cyclosystems are placed laterally and alternately on the small branches, that the cyclosystems show from 8 to 17, generally 9 to 11 dactylopores, and that the gastrostyle is almost spherical, with equal height and breadth. The characters here cited from BROCH'S description are almost exactly those of the species *Stylaster erubescens* as described and figured by POURTALES (1871). BROCH'S figures of colonies in natural size (1914, Pl. 1, Figs. 8 and 9, Pl. 2, Figs. 10 and 11) represent corals with an entirely similar form of growth as the specimen of *Stylaster erubescens* of POURTALES (1871, Pl. 4, Fig. 10); moreover, the figures of enlarged terminal branches (POURTALES, 1871, Pl. 4, Fig. 11; BROCH, 1914, Pl. 2, Fig. 17) are strikingly similar.

Unfortunately BROCH gave the name *Stylaster roseus* to the corals here dealt with, while placing the name *Stylaster erubescens* in the synonymy of the species. In BROCH'S paper there is an instructive figure of a longitudinal section (1914, Pl. 3, Fig. 22) showing in two of the cyclosystems the spherical gastrostyles, which, judging by this figure, have a height and a breadth of about 0·3 mm. This figure has been copied in other publications (BROCH, 1924; KÜHN, 1939) as a longitudinal section of a branchlet of *Stylaster roseus* (Pallas).

BROCH (1914, p. 15) remarks " As the species is the commonest Stylasterid in the Atlantic north of the equator, it is probably the same form that served as a basis for Pallas' description of *Madrepora rosea* "; this is right as far as the specific identity of the North Atlantic corals with *Stylaster erubescens* is concerned, but it was an error to identify this species with *Stylaster roseus*. POURTALES (1868, p. 136, footnote; 1871, p. 83) examined the two forms and referred to them as separate species, the one from shallow water, the other from deeper water only; it is to be regretted that he did not give a description of the specific characters of *Stylaster roseus*.

The conclusion of the data dealt with above is that *Stylaster roseus* (Pallas), the type species of its genus, has a rather complicated history. The descriptions and figures of the various eighteenth-century authors contain some characters which may be considered typical of the species. In later years these older data were overlooked and the name *S. roseus* was given to corals which in reality belong to the species *Stylaster erubescens* Pourtalès. An examination of specimens from shallow water of the island Curaçao could lead to additional characters, especially those of the gastrostyle, proving that the species *Stylaster roseus* is distinct from all the later described species of the genus.

REFERENCES

Broch, Hj. (1914), Stylasteridae. *Danish Ingolf Exped.*, Copenhagen, **5** (5), 1–25.

Broch, Hj. (1924), Hydroida. In: Handbuch der Zoologie (Kükenthal-Krumbach), Berlin & Leipzig, **1**, 422–458.

Esper, E. J. C. (1794–1797), Fortsetzungen der Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. Nürnberg, **1**, 1–230.

Gray, J. E. (1831), Description of a new genus of star-bearing corals. The Zoological Miscellany, London, 1–80.

Houttuyn, M. (1772), De Zee-Gewassen. Natuurlyke Historie . . . volgens het Samenstel van den Heer Linnaeus. Amsterdam, **1** (17), 1–613.

Kühn, O. (1939), Hydrozoa. In: Handbuch der Paläozoologie (Schindewolf). Berlin, **2A**, 3–68.

Lamarck, J. B. P. A. de (1816), Histoire naturelle des animaux sans Vertèbres. Paris, **2**, 1–568.

Milne Edwards, H. and Haime, J. (1850), Recherches sur les Polypiers; 5me mém. Monographie des Oculinides. *Ann. Sci. Nat.*, (3), *Zool.*, **13**, 63–110.

Milne Edwards, H. (1850–1854), A monograph of the British fossil corals. London, i–lxxxv, 1–322.

Moseley, H. N. (1880), Report on certain Hydroid, Alcyonarian, and Madreporarian Corals procured during the voyage of H.M.S. *Challenger*, in the years 1873–1876. *Rept. Sci. Res., Challenger, Zool.*, **2** (1), 1–248.

Müller, P. L. S. (1775), Von den Corallen. Des Ritters Carl von Linné . . . vollständiges Natursystem. Nürnberg, **6** (2), 641–960.

Pallas, P. S. (1766), Elenchus Zoophytorum. Hagae-Comitum, i–xxviii, 1–451.

Pourtalès, L. F. de (1868), Contributions to the fauna of the Gulf Stream at great depths (2nd series). *Bull. Mus. Comp. Zoöl., Harvard Coll.*, **1** (7), 121–141.

Pourtalès, L. F. de (1871), Illustrated catalogue of the Museum of Comparative Zoölogy at Harvard College, No. 4. Deep-sea Corals. Cambridge, 1–93.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 139-148.

External metabolites in the sea

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With the exception of a hint or two before the turn of the century, by such prophets as Brandt and Nathansohn, it was not until the inter-war period that marine workers began to turn their minds to the possible existence of more subtle ecological relationships than those imposed on organisms by their inanimate environment and by predators. It is relevant that Knörrich and Pütter had postulated the direct food value of dissolved organic food substances in the sea, although this view appeared to be finally rejected by Krogh (1931); however, such possibilities are not the main subject of this paper, although they may once again demand investigation. But those who drew our attention once more to the other possible significance of dissolved organic matter deserve our gratitude. Quite the most senior of those now living was Henry Bigelow who said in his famous book *Oceanography*, among many other stimulating things, " as yet we know little of the inter-relationships of different species or groups of animals in the sea beyond the obvious fact that some prey on others, but we may be certain that in many cases inter-relationships of less obvious sorts are vital links in the animal economy " (Bigelow, 1931, p. 131, quoted by Russell, 1936). Before many years elapsed, it seemed clear that he was right and we now know that he was! For the volume in his honour, it is fitting to pay tribute to his foresight.

It would not be proper on this occasion, however, to ignore the others: from Johnstone, Scott and Chadwick (1924)[*] to Allee (1931)[†] and Hardy (1935)[‡]. All were feeling towards the certainty of a new type of relationship in ecology, and particularly marine ecology, for which there was then all too little evidence (although it may now seem striking that it was around this very time, in 1929, that the late Sir Alexander Fleming was making his first observations on the antibiotic influence of Penicillium). It was the stimulus of such hints, and particularly that of working with Hardy when he was evolving his idea of " animal exclusion ", that led Lucas to gather an odd collection of references in support of a speculative theory of " non-predatory " relationships—based on the release and biological influence of metabolites ranging from " toxins to vitamins and hormones " (Lucas, 1938).

This evidence ranged from the effects of external metabolites in the field of bacteriology, through some of the " mass physiology " experiments of Allee's school, to the speculations of AKEHURST (1931) about the temporal alternation of oil-producing and starch-producing algae in ponds, and some tentative experiments (LUCAS, 1936) regarding " animal exclusion ". With these were coupled ALLEN and NELSON'S pioneer demonstrations (1910) of the need for some accessory substances in diatom culture; the use of " soil solution " for more effective growth; and GRAN'S observations (1931) on the relatively intensive growth of phytoplankton at the junction of two bodies of water. But more evidence was needed.

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[*] " Also, we are pretty sure that the plankton communities influence each other—that there are what we may call group symbioses on the great scale so that the kind of plankton which we may expect to be present in a certain sea-area must depend, to some extent, on the kind of plankton which was previously present."

[†] " Once formed, aggregations of aquatic organisms condition the medium surrounding them by the addition of secretions and excretions, the nature and biological effect of which form one of the important problems of mass physiology."

[‡] Hardy postulated a " presumably chemical " basis for his theory of " animal exclusion ", and also speculated upon the " biological history " of waters, e.g. the changes which may occur in water passing from regions of predominantly " free " phyto-plankton to regions of " imprisoned " phyto-plankton.

More evidence did in fact exist, scattered widely through the field of biological research, and work during the war brought even more, particularly that associated with antibiotics. It thus became possible to review a wider field and to formulate the concept more precisely (LUCAS, 1947, and from a more general ecological viewpoint, 1949). In the aquatic field reference was made, among others, to the very different growth-rates of diatoms cultured in different natural sea waters (MATSUDIARA, 1939; HARVEY, 1939), and HARVEY'S associated investigations of the effects of various accessory substances on growth; to other examples of the influence of waters previously containing living organisms (or their by-products) upon different organisms in culture (e.g. LEVRING, 1945); and to Fox's demonstrations of the occurrence of carotenoids free in natural waters and their deposits (e.g. 1944). When supported by the rapidly increasing knowledge from the various fields of microbiology, together with a wide range of other biological references, it seemed not unreasonable to come to conclusions along the following lines:

" (1) It is characteristic of cells to liberate certain metabolites, and these are known in a variety of instances to have great influence as endocrines.

" (2) It is now well known that a number of these potent metabolites are eliminated as secretions or excretions by the organisms themselves, and many other chemicals are eliminated which are not yet known to have any specific effects within the body.

" (3) Particularly insofar as any of these metabolites are . . . parts of the environment of other organisms, they may be expected to have immediate potency for many of them. . . . The term ' ectocrines ' has been suggested for such metabolites.

" (4) More generally, however, . . . the capacity for adaptation of most organisms suggests that further differentiation between beneficial and antagonistic relationships would be likely to have developed between the producers and those affected. In the extreme instances escape, exclusion, or death must be expected on the one hand, and obligatory association (parasitism, symbiosis) on the other.

" (5) Such processes are believed to be important in evolution, and they are considered to mediate communal relationships in ecology, which is the contemporary aspect of evolution. They should be seen as part of the nexus which also includes physical and chemical relationships as well as those of prey and predator " (LUCAS, 1949, pp. 353–354).

If these seemed then to be rather premature speculations, they now have much more specific support. It is not possible to review the whole field here and this note is simply intended to bring together a few references indicating some of the lines along which progress is now being made. However, the suggestions could properly be regarded as stemming from, and partly supported by, the theory of " animal exclusion ", and evidence (BAINBRIDGE, 1952) has recently been brought to bear against the only laboratory experiments (LUCAS, 1936) specifically made to investigate that theory. It seems necessary, therefore, to mention BAINBRIDGE'S experiments first, and it is particularly appropriate that they were made by one who has worked with both HARDY and LUCAS. LUCAS concluded that his very preliminary experiments were not inconsistent with HARDY's theory and, indeed, appeared to offer support for it. The work had to cease and they went no further than that. BAINBRIDGE's work was not only more detailed but much more precisely executed, and it represents a real contribution to our knowledge of the prey-predator relationship. His criticism of LUCAS's " light and dark " experiments is that they simply reflected the tropism of the animals—a possibility discussed by LUCAS. It is and always was relevant. For all that, the very weaknesses in LUCAS's work and the greatly improved techniques in BAINBRIDGE's are very relevant, and they may still mean that BAINBRIDGE's results are not necessarily so critical of the theory of animal exclusion as they seemed at first sight.

BAINBRIDGE was careful to use only algal cultures aged not more than " a week or so " (his p. 391) after inoculation, whereas LUCAS probably seldom used such fresh cultures in his work. Indeed, LUCAS's cultures may, in the light of modern ideas (many of his experiments were made in 1934), have been approaching senescence at times and, whatever may be their potency during the early phase of a culture, we can now see that metabolites released during the later stages (e.g. PRATT, 1943) may well have been harmful and have acted more as deterrents than as attractions. This is, of course, far from certain and exploratory experiments on these lines would be useful. In any event, it is also relevant that, whilst BAINBRIDGE found that most of his plankton animals were attracted by, or at least did not appear to avoid, the majority of the denser phytoplankton cultures, several were either neutral or were markedly avoided or even lethal. Two of the more " harmful " were flagellates. It is also significant that not only did most of his cultures influence the animals but, in several experiments, so did the culture fluids in the absence of the plant cells. The main conclusion is that his experiments demonstrated the release by plant cells of substances which were frequently attractive and occasionally repellent to many of his animals (BAINBRIDGE, 1952, p. 429). Like LUCAS, also, he found evidence of an optimum density of plant cells below and above which the animals were presumably either starved or poisoned.

However, other evidence was accumulating. In the first place, there was the work of LWOFF's school (1943), which demonstrated convincingly the release of " vitamins " into their environment by some micro-organisms, and the vital need for such vitamins by some other forms which are unable to synthesize them. LWOFF saw this as evidence of a progressive loss of physiological function during evolution, but it provided also a mass of evidence of mainly beneficial inter-relationships, mediated by the release of metabolites potentially of communal significance.

Next there is the work of LEFÈVRE and his school (1952) which, while collectively reviewed under the title of " Auto. et hétéroantagonisme chez les algues d'eau douce ", demonstrates also quite clearly the very real influence, both favourable as well as unfavourable, which one micro-organism may exert upon others through the mediation of its secretions or excretions. In brief, these workers concluded that the three groups of bacteria, algae and fungi, all have " Faculté d'élaborer des substances actives autoantagonistes, hétéroantagonistes ou favorisantes. Spécificité des substances actives produites. . . . Décharge rapide des substances accumulées par les cellules quand on les replace dans un milieu neuf. . . . Solubilité des substances actives dans l'eau ou dans certains solvants organiques. . . . D'autre part, il n'est pas impossible que les substances actives produites par des Algues se developpant massivement dans une collection d'eau aient une influence directe sur la multiplication et le développement des animaux aquatiques: Entomostracés, Insectes, Mollusques, Vermes et peut-être même Poissons " (Lefèvre, Jakob and Nisbet, 1952).

The limitations implied by the title of their paper and the wider relevance of the text (summarized on their pages 173–181) are not without interest, for there seems to have been a strong tendency on the part of various workers to anticipate unfavourable reactions rather than favourable ones in given circumstances; e.g. the review by McCombie, 1953, mentions only the possibility of harmful effects of free metabolites,* while one or two workers, in referring to Lucas' papers, have noticed only his references to harmful effects. The fact is that one organism's " meat " may be another's " poison " in the ecological nexus, and terms such as " harmful " and " beneficial " can only be used in an immediate and limited sense. In this sense, much of the evidence demonstrates the development of " favourable " relationships, although admittedly some of the most striking are unfavourable. One of the latter is instanced by the phenomenon of " red tide ", with its harmful effects on marine animals and unfortunate repercussions on man. Lucas instanced such effects of the secretions of plants or animals, and much more evidence has been accumulated since (e.g. Brøngersma-Saunders, 1948). There is now no doubt that, even though in their more striking forms such phenomena can be regarded as abnormal, they are, in fact, far from unusual in a lesser degree and, further, they are mediated by the release of " toxic " substances, frequently by flagellates. Their nature and the more precise conditions which lead to their production in a mild or extreme form, are being intensively investigated in several laboratories.

The major task now is to determine the nature and effects of some of the more significant metabolites in aquatic ecology, to trace their probably variable distribution in some natural waters, and to determine the conditions leading to their production. Several lines of work have recently been developed. In the United States, Pratt (1943) has produced clear evidence that *Chlorella* cells in culture release a growth inhibiting substance, whilst Rice (1954) has grown *Chlorella vulgaris* and *Nitzschia frustulum* (both fresh water algae) together, and demonstrated clearly that neither grows so satisfactorily in the company of the other as it does in pure culture (depending upon the size of the populations used). Each was similarly inhibited when grown in the culture medium of the other, after its cells had been removed by filtration, and both were also inhibited when grown in a culture medium prepared with pond water which had supported a dense growth of *Pandorina* before filtration. Again, the metabolites in solution could be absorbed in charcoal and removed by autoclaving, suggesting volatile substances.

Harvey, at Plymouth, following on his pioneer culture experiments with growth substances, is now attempting to review all the evidence available so as to define more rigorously than has previously been possible the precise requirements of phytoplankton organisms in nature and in culture. Meanwhile, PROVASOLI, HUTNER, and their colleagues at the Haskins Laboratories, have also very rightly undertaken fundamental and precise experiments on the basic requirements for the growth of marine and fresh water micro-organisms. PROVASOLI and PINTNER (1953), in their review of the ecological implications of the nutritional requirements of algal flagellates, have brought together a large number of references to the need of various micro-organisms for growth factors and trace elements. To these they have added the striking results obtained in their own laboratory. The evidence ranges from the early demonstration by HUTCHINSON (1943) of the actual existence of thiamin in natural waters, to the significant requirement of various forms for cobalamin (vitamin B_{12}) in pure culture within chemically defined media. Of particular importance is the rigorous technique, necessary and adopted, in their work. All the results to date demonstrate aspects of " non-predatory " relationships. As they say:

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* Lucas drew attention to this tendency (1944 and later) in respect of the term " antibiotic ". He pointed out that not only were antibiotics necessarily favourable to those organisms, such as man, which are preyed upon by the object of antibiosis, but that the antibiotic might well prove beneficial to those organisms succeeding its producer in the ecological chain (just as Akehurst, 1931, had suggested the autotoxic secretions of one algae may be beneficial for its successors). Indeed, the ecological successors of the producers of antibiotics can only succeed by virtue of being adapted to the presence of the antibiotics or their degradation products, and there is already some evidence that this may be true even for a potent substance such as penicillin. Here is a possible theoretical basis for ecological succession.

" It is a reasonable assumption that if an organism requires a growth factor *in vitro*, then this metabolite or its physiological equivalent should be found in significant amount in the environment " (p. 845).

" The water environment is the one in which metabolites are interchanged most efficiently. It is to be expected that the interdependent growth of the different groups of water organisms should sensitively reflect the excretion and consumption of metabolites. Undaunted by new intricacies, we should envisage all the possibilities in these relationships, and not hesitate to follow LUCAS's lead in constructing theoretical frameworks upon which to hang data. In the present paper, only a few aspects of the nutrition of phytosynthetic forms are considered. It is possible, nevertheless, to state more definitely some of the interdependencies based upon ' external metabolites ': (1) the interchange of growth factors; (2) the lowering of inhibitory concentrations of several major mineral nutrients, especially PO_4; and (3) the preferential utilization of minerals, including trace metals, may condition waters, bringing their concentrations into the optimal zones for succeeding forms. The practical aim—to predict algal successions and blooms—may be achieved through a comprehensive knowledge of vitamin cycles as well as mineral cycles. An immediate problem is to trace the thiamine and cobalamin cycles " (p. 849).

DROOP (for example, 1954) is pursuing a similar course at Millport, in Scotland, and has shown the need of several marine flagellates* for vitamin B_{12}. LEWIN, in Canada, has also found B_{12} essential for the growth of the alga *Stichococcus* in sea water (1954). The presence of free B_{12} in natural sea water has been demonstrated, and its distribution is being examined in more than one laboratory. DROOP is now developing an assay for it in sea water. Along a rather different line FOGG (1952) has suggested that some at least of the external metabolites (for instance, the polypeptides of blue-green algae) may further communal growth, via chemical linkage, by making relatively insoluble nutrients available in a form more suitable for assimilation.

Turning now to the animal field, several workers have followed ALLEE in linking aggregations with the release of metabolites (for example, COLE and KNIGHT-JONES, 1949, and KNIGHT-JONES, 1950). Again, there was the demonstration by ALLISON and COLE (1935) that the feeding movements of barnacles can be correlated with the

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*Droop has now demonstrated this need in the diatom *Skeletonema costatum* (DROOP 1955).

abundance of dinoflagellates in the water (with the postulate that this is mediated by a by-product) and the subsequent hint (MIAZAKI, 1938) of the effect of an alga upon the spawning of the male oyster. Now, COLLIER and his colleagues, at Galveston, Texas, have moved into this field from a rather different angle. Whilst studying the effects of industrial wastes on oysters, they deduced a generalized influence upon their pumping rates, which was found in due course to be correlated with the presence or absence in the water of a carbohydrate-like substance; this is either truly soluble or colloidal, and may attain densities in neritic waters of up to 25 mg/l (COLLIER, RAY, MAGNITSKI and BELL, 1953). During further work (COLLIER, 1953) they found that, along with tyrosine-tryptophane, these carbohydrates have a marked diurnal variation in abundance, and their production is associated with light and aeration—so that they are probably the by-products of plant growth. In addition, a rhamnoside (WANGERSKY, 1952) has been isolated from oceanic water, and particularly from " red tide " water up to quantities of 50 mg/l, whilst minute quantities of ascorbic acid and some other carbohydrates of very low molecular weight are being isolated for identification. The significance of such substances to the oyster may be two-fold, but it is at least clear that one of the substances in question is both widespread and very variable in quantity, and that it acts as a remarkably effective (and almost instantaneous) pumping stimulus. It would appear that the substance is also absorbed by the oysters (up to 50 mg per hour), although it remains to be seen whether such substances are of positive and substantial food value (see, for example, KORRINGA, 1949, and JØRGENSON, 1952)—a possibility which would greatly have interested both PÜTTER and KROGH—or whether their role is limited to providing sensory stimuli and perhaps growth factors. At the moment, the chief point is that they " found a biologically active compound (or group of compounds) to which an organism would respond quantitatively ", and drew attention to the link between this work and the probable significance of external metabolites or " ectocrines ".

Work being undertaken by WILSON, at Plymouth, is also relevant. For many years he has been concerned with the problems of breeding and growing planktonic larvae, particularly polychaetes. On the one hand he noticed that sands from some areas were more suitable for the settlement of polychaete larvae than others (e.g. WILSON, 1948 and 1953) whilst, on the other hand, he found that, with the passage of years, his success with rearing these and other larvae was tending to decrease (WILSON, 1951). Continued and painstaking investigations in various directions now seem to make it clear, however, that the suitability of sands for larval settlement must be determined by the existence on them of other forms of life, probably micro-organisms—" Organic material, living or dead, on the sand grains plays an important role in rendering a sand attractive or repellent to the larvae " (WILSON, 1954). Whilst we may not be so obviously concerned here with a free metabolite (although that is quite possible), we have to deal once again with the significance for living larvae of organic remains, and *with their detection* by these larvae.

The other instance is of even more direct interest. WILSON associated his decreasing success with the now familiar change known to have taken place whereby the waters of the English Channel have been much less productive since 1930 than in the 1920s. Superficially, this was due to reduced phosphate content, but the possibility of more subtle factors remained, and comparative experiments were made by rearing polychaete and echinoderm larvae in (a) " local " Channel water collected in the Plymouth neighbourhood (as had been usual) and (b) water collected from the Celtic Sea, in which the typical plankton community is normally similar to that of the " local " water before 1931. The results were striking; good growth of polychaete and echinoderm larvae was obtained in the latter and only poor or deformed growth in the former. Appropriate combinations of experiments suggested the presence of a " beneficial " substance in the Celtic water, and its lack in the local water, rather than the existence of a harmful substance in the latter. More recent work has shown that Clyde water also tends to be more suitable than " local " Channel water and, although there are variations, the inferences seem to be unambiguous. In association, WILSON and ARMSTRONG (1954) have shown that heating the waters for shorter or longer periods generally had an adverse effect on the larvae bred in them, thus suggesting the existence of a beneficial substance of a more or less volatile nature. Their analyses have not yet been carried to the stage of demonstrating any particular component or fraction which is responsible for the biological difference.

Recently, at Aberdeen, JOHNSTON has extracted various fractions of the organic matter in natural sea waters, and made some preliminary biochemical analyses. Certain of these were tested in bio-assay on a number of phytoplankton diatoms and flagellates (with results summarized by JOHNSTON in his Table I, 1955, from a paper read to the International Council for the Exploration of the Sea in 1954). It was found that the growth of many was favoured and of some others hindered relative to controls, although, " since the tests were limited to one concentration, further (and perhaps different) instances of these effects would probably have been observed by testing a range of concentrations. One particular fraction was found to promote greater growth in 9 of the 11 species tested." The initial information so gained is providing a basis for the bio-assay of sea water samples from different areas, with a view to a preliminary labelling of such waters according to their physiological effects. Then, further attention will be given as far as possible to identifying some of the substances thus found to be of biological significance. JOHNSTON tentatively discusses the possible value of such information to the fisheries worker.

In all such experimental work, tribute should be paid to the surveys made by RUSSELL (e.g., 1939) and FRASER (e.g., 1952). By distinguishing on biological evidence between water masses, which have often been indistinguishable on familiar hydrographical criteria, they are providing the experimenter and biochemist with invaluable clues.

In conclusion, it can be said that, before the war, a few people were moving towards a conception of ecological inter-relationships which seemed likely to be an important complement to the already familiar relationships existing between the organism and its physical environment, and those between prey and predator. Limited observations in diverse fields suggested that these non-predatory relationships would be mediated by the release of metabolites of varying potency for other members of the community. Further work during the war made it possible to gather much more support for the suggestion, and it is now quite clear that dissolved or colloidal organic matter may be present in natural fresh and marine waters in greater quantities than was originally envisaged. Indeed, it is still uncertain whether these may not in themselves provide, for some forms, nutrients in the ordinary sense of the word*. It is also clear that within this general heading of organic matter are included, sometimes in very minute quantities, substances whose effects within the community may not unreasonably be compared with those of endocrine metabolites within the body. It now seems necessary to believe that such substances play a considerable part in the growth of aquatic communities of bacteria, algae and fungi (we still have much to learn of the activities of the last in natural waters), so that the success of various organisms, and consequently their ecological succession, may be largely determined in this way. The next point is that we now have a number of instances in which such free metabolites affect not only the lives of protozoans (whose communal life may be expected to be very similar to that of the micro-plants, except in so far as their need for external metabolites can be expected to be much greater), but also those of higher animals such as worms, echinoderms and molluscs and probably crustaceans. We can confidently expect this list to be extended, probably even to include fish.

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*See, for example, MORRIS, 1955.

For example, HASLER and WISBY (1951) have obtained most interesting evidence of the influence of different natural waters upon the movements of fish. They found that minnows were able to discriminate between the waters of two Wisconsin creeks after as little as two months conditioning, while cautery of their olfactory epithelia rendered them unresponsive to conditioning. It appeared, therefore, that olfaction was the principal, if not the sole, means of discrimination. They further demonstrated that the chemical response was not to carbon-dioxide in the creek waters, for example, but that the significant fraction was probably organic, in the usual sense, in that the minnows reacted to the distillate rather than the residue (vacuum distillation at 25° C), so that the existence of a volatile substance in the water can be anticipated. Here then is the essence of one reaction system on which " homing ", and perhaps other aspects of migration, might reasonably be based. Indeed, HASLER's preliminary tests suggest that salmon can detect such " odours " of streams and discriminate between them. In that instance, it would be necessary to imagine the salmon being conditioned during its early fresh water life to the " odours " of the " home " tributary. HASLER has also been able to demonstrate that minnows could respond to such odours after " forgetting periods " which were longer in fishes trained when young than in old ones. It may not therefore be so unreasonable to think of such reactions as even applying to the movements of other and wholly marine fish.

Lastly, when mentioning this particular possibility as one of the possible uses to which such fundamental research might ultimately be put in a fisheries laboratory, JOHNSTON (1955) also referred to the possibility that " fertilization " of natural waters, normally by enrichment with phosphates and nitrates, might come to include the addition of minute amounts of critical metabolites. Ideally, at least, these would be selected as those likely to mediate the succession of " desirable " algae in relation to the favoured crop. For example, it has seemed at times that the risks of fertilization being followed by blooms of " undesirable " algae are considerable, but it does not seem unreasonable to imagine that such a succession could, to some extent, be controlled if the fertilizer included not only normal manures but a specific metabolite antagonistic to these algae and preferably favouring other forms. Indeed, it may not be too speculative to suggest that some natural waters, normally producing little in the way of a desirable crop, might be induced to undergo a complete ecological change by the addition of a critical metabolite alone. The apparent scarcity of nutrients in some of these waters may not be so significant as it may seem. Not only may there be great reserves of nutrient in the bottom deposits but, as the Haskins Laboratories have demonstrated, many algae can tolerate only quite dilute nutrient solutions, and can thrive on them, so long as the necessary free metabolites are present. Perhaps particularly in some " barren " fresh waters, it may be that certain types of ecological development are blocked, just as in some laboratory experiments, by the natural absence of a specific metabolite essential to the life of an essential organism in fish management.

Such possibilities as these various lines of work indicate may make this field an attractive one to fisheries worker and biologist alike. Certainly, considerable development can be expected during the next few years. A number of those working in the various fields, however, may possibly have missed something of the community of interest they share with many others. With a few striking exceptions, what now seem to be very relevant cross references are frequently missing from bibliographies. Perhaps this paper may serve to emphasize, where necessary, some of the fundamental features thought to be common to the various investigations.

REFERENCES

Akehurst, S. C. (1931), Observations on pond life, with special reference to the possible causation of swarming of phytoplankton. *J. Roy. Micr. Soc.*, **51,** 237–265.

Allee, W. C. (1931), *Animal aggregations*. Univ. Chicago Press, 431 pp.

Allen, E. J. and Nelson, W. E. (1910), On the artificial culture of marine plankton organisms. *J. Mar. Biol. Assoc., U.K.*, **8,** 421–474.

Allison, J. B. and Cole, W. H. (1935), Behavior of the barnacle *Balanus balanoides* as correlated with the planktonic content of the sea water. *Bull. Biol. Lab., Mt. Desert Is.*, 24–25.

Bainbridge, R. (1953), Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Assoc., U.K.*, **32,** 385–447.

Bigelow, H. B. (1931), *Oceanography*. Houghton Mifflin Co., 263 pp.

Cole, H. A. and Knight-Jones, E. W. (1949), The setting behaviour of larvae of the European flat oyster, *Ostrea edulis* L., and its influence on methods of cultivation and spat collection. *Min. Agric. and Fish., Fish. Invest.*, (2), **17** (3), 1–39.

Collier, A. (1953), The significance of organic compounds in sea water. *Trans. N. Amer. Wildlife Conf.*, **18,** 463–472.

Collier, A., Ray, S. M., Magnitski, A. W. and Bell, J. O. (1953), Effect of dissolved organic substances on oysters. *U.S. Fish and Wildlife Serv., Fish. Bull.*, **54** (84), 167–185.

Droop, M. R. (1954), Cobalamin requirements in Chrysophyceae. *Nature*, **174,** 520–521.

Droop, M. R. (1955), A pelagic marine diatom requiring cobalamin. *J. Mar. Biol. Assoc.*, U.K. **34,** 229–231.

Fogg, G. E. (1952), The production of extracellular nitrogenous substances by a blue-green alga. *Proc. Roy. Soc.*, (B), **139,** 372–397.

Fox, D. L. (1944), Fossil pigments. *Sci. Mon.*, **59,** 394–396.

Fraser, J. H. (1952), The Chaetognatha and other zooplankton of the Scottish area and their value as biological indicators of hydrographical conditions. *Scottish Home Dept., Mar. Res.*, 1952 (2), 1–52.

Gran, H. H. (1931), On the conditions for the production of plankton in the sea. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **75,** 37–46.

Hardy, A. C. (1935), Part V. The plankton community, the whale fisheries, and the hypothesis of animal exclusion. In: Hardy, A. C. and Gunther, E. R. (1935), The plankton of the South Georgia Whaling Grounds and adjacent waters, 1926–1927. *Discovery Repts.*, **11,** 1–456.

Harvey, H. W. (1939), Substances controlling the growth of a diatom. *J. Mar. Biol. Assoc., U.K.*, **23,** 499–520.

Hasler, A. D. and Wisby, W. J. (1951), Discrimination of stream odors by fishes and its relation to parent stream behavior. *Amer. Nat.*, **85,** 223–238.

Hutchinson, G. E. (1943), Thiamin in lake waters. *Arch. Biochem.*, **2,** 143–150.

Johnston, R. (1955), Biologically active compounds in the sea. *J. Mar. Biol. Assoc., U.K.* **34,** 185–195.

Johnstone, J., Scott, A. and Chadwick, H. C. (1924), *Marine Plankton*. Liverpool Univ. Press, 194 pp.

Jørgensen, C. B. (1952), On the relation between water transport and food requirements in some marine filter feeding invertebrates. *Biol. Bull.*, **103,** 346–363.

Knight-Jones, E. W. and Stevenson, J. P. (1950), Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *J. Mar. Biol. Assoc., U.K.*, **29,** 281–297.

Korringa, P. (1949), More light upon the problem of the oyster's nutrition. *Bijdr. Dierk.*, **28,** 237–248.

KROGH, A. (1931), Dissolved substances as food of aquatic organisms. *Biol. Rev.*, 6, 412–442.

LEFÈVRE, M., JAKOB, H. and NISBET, M. (1952), Auto. et hétérochez les algues d'eau douce. *Ann. Sta. Cent. Hydrobiol. Appl.*, **4**, 5–198.

LEVRING, T. (1945), Some culture experiments with marine plankton diatoms. (*Medd. Oceanogr.. Inst., Göteborg*, 9.) *Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handl.*, **3** (12), 1–18.

LEWIN, R. A. (1954), A marine *Stichococcus* sp. which requires vitamin B_{12} (Cobalamin). *J. Gen. Microbiol.*, **10** (1), 93–96.

LUCAS, C. E. (1936), On certain interrelations between phytoplankton and zooplankton under experimental conditions. *J. du Cons.*, **11**, 343–362.

LUCAS, C. E. (1938), Some aspects of integration in plankton communities. *J. du Cons.*, **13**, 309–322.

LUCAS, C. E. (1944), Excretions, ecology and evolution. *Nature*, **153**, 378.

LUCAS, C. E. (1947), The ecological effects of external metabolites. *Biol. Rev.*, **22**, 270–295.

LUCAS, C. E. (1949), External metabolites and ecological adaptations. *Symp. Soc. Exp. Biol.*, **3**, 336–356.

LWOFF, A. (1943), L'evolution physiologique. *Actualités Sci. Industr.*, 970, H. Hermann, Paris.

MCCOMBIE, A. M. (1953), Factors influencing the growth of phytoplankton. *J. Fish. Res. Bd., Canada*, **10** (5), 253–282.

MATSUDIARA, T. (1939), The physiological property of sea water considered from the effect upon the growth of diatoms, with special reference to its vertical and seasonal change. *Bull. Japan. Soc., Sci. Fish.*, **8**, 187–193.

MIYAZAKI, I. (1938), On a substance which is contained in green algae and induces spawning action of the male oyster. (Preliminary note.) *Bull. Japan. Soc., Sci. Fish.*, **7**, 137–138.

MORRIS, R. W. (1955), Some considerations regarding the nutrition of marine fish larvae. *J. du Cons.* **20** (3), 255–265.

PRATT, R. (1943), Studies on *Chlorella vulgaris.* VI. Retardation of photosynthesis by a growth-inhibiting substance from *Chlorella vulgaris. Amer. J. Bot.*, **30**, 32–33.

PROVASOLI, L. and PINTNER, I. J. (1953), Ecological implications of *in vitro* nutritional requirements of algal flagellates. *Ann. N.Y. Acad. Sci.*, **56**, 839–851.

RICE, T. R. (1954), Biotic influences affecting population growth of planktonic algae. *U.S. Fish and Wildlife Serv., Fish. Bull.*, **54** (87), 227–245.

RUSSELL, F. S. (1936), A review of some aspects of zooplankton research. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **95**, 5–30.

RUSSELL, F. S. (1939), Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. *J. du Cons.*, **14** (2), 171–192.

WANGERSKY, P. J. (1952), Isolation of ascorbic acid and rhamnosides from sea water. *Science*, **115**, 685.

WILSON, D. P. (1948), The relation of the substratum to the metamorphosis of *Ophelia* larvae. *J. Mar. Biol. Assoc., U.K.*, **27**, 723–760.

WILSON, D. P. (1951), A biological difference between natural sea waters. *J. Mar. Biol. Assoc., U.K.*, **30**, 1–20.

WILSON, D. P. (1953), The settlement of *Ophelia bicornis* Savigny larvae. *J. Mar. Biol. Assoc., U.K.*, **31**, 413–438.

WILSON, D. P. (1954), The attractive factor in the settlement of *Ophelia bicornis* Savigny. *J. Mar. Biol. Assoc., U.K.*, **33**, 361–380.

WILSON, D. P. and ARMSTRONG, F. A. J. (1954), Biological differences between sea waters: experiments in 1953. *J. Mar. Biol. Assoc., U.K.*, **33**, 347–360.

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A revision of Ernst Haeckel's determinations of a collection of Medusae belonging to the Zoological Museum of Copenhagen

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Summary—The collection of medusae sent from the Zoological Museum of the University of Copenhagen to ERNST HAECKEL for identification comprised 231 numbers; from 166 of these the specimens are still in our collection and are the subject of this revision.

Specimens from 12 localities were not identified with certainty by HAECKEL; they belong to 9 different species, 6 of which are described in previous literature, whereas 3 species have been described after the publication of HAECKEL's monograph.

In the collection and the accompanying list 54 species are provided with generic and specific name in HAECKEL's hand-writing. After the revision the actual number of species is reduced to 37.

26 species are designated as new and are represented by their type-specimens or cotypes; 5 of these may be retained as valid species, 3 of them with unaltered generic name; the remaining 21 of HAECKEL's new species belong to 15 species previously described.

Among the 28 species, which are not marked as new, 10 are synonyms, and 8 are erroneously identified.

WHILE ERNST HAECKEL prepared his famous monograph, " Das System der Medusen ", which was published in 1879–80, he borrowed the whole collection of medusae belonging to the Zoological Museum of the University of Copenhagen. The Danish zoologist JAPETUS STEENSTRUP had organized a fruitful collecting of marine animals, particularly pelagic ones, by officials in Greenland (inspector OLRIK and others) and captains and physicians on Danish merchant vessels (ANDREA, BANG, HOLBÖLL, HYGOM, etc.) on their journeys to Greenland, the West Indies, South America, India and China. The result was that, until the far-going oceanographical expeditions began with the cruise of the *Challenger* in 1873–76, the museum in Copenhagen possessed one of the greatest collections of marine animals in the world.

The collection of medusae was sent to HAECKEL in Jena accompanied by a detailed list written by CHR. LÜTKEN with (1) provisional determinations by STEENSTRUP and LÜTKEN, (2) localities, (3) names of collectors, (4) an empty column, in which HAECKEL wrote his own determinations of the species. The list, which contains 231 numbers, is still in our museum and is a document of great value, giving us the names of all the species in HAECKEL's own hand-writing (see Fig. 1). The majority of specimens are also still in our collection. Many of them are in a fairly good condition, though they must be handled with care, because they are more or less brittle in consequence of their being preserved in alcohol.

Many of the species described or recorded by HAECKEL have been the subject of much discussion, and it has often been desirable to re-examine the original specimens. It is not to be denied that HAECKEL's artistic temperament and fertile imagination sometimes led him to construct a detailed description and beautiful drawings from an ugly and mutilated specimen. But he also had excellent powers of observation, and when his descriptions and figures are based on living or tolerably well-preserved specimens, they are usually reliable, though sometimes one must wonder at what he has overlooked (e.g. in " *Hippocrene platygaster* " and " *Thaumantias eschscholtzii* ", see below).

Occasionally some of the specimens in the Copenhagen collection have been re-examined, partly by me (KRAMP, 1919; 1926; 1947, specimens from the northern Atlantic), partly by CL. HARTLAUB (1913, northern Pandeidae) and by G. STIASNY (1922 A, some East-Asiatic Scyphomedusae). Remarks on some tropical Atlantic forms will also be published by me in the near future (*Atlantide* Reports and *Discovery* Reports, in press).

A revision of the whole collection may, however, be useful to future workers on medusae, and in the present paper I shall give a complete list of that part of the old collection which is still in existence. Fortunately, as seen from the list, none of the specimens, which have disappeared, belonged to species which are not represented in the preserved collection. The succession of the species follows the order in which they are mentioned in HAECKEL's monograph and with HAECKEL's generic and specific names as head-lines, with the exception of the Narcomedusae, none of which were finally determined by him. In square brackets [ ] is added the correct name of each species as found by the revision, in so far as it differs from the name given by HAECKEL, or in cases where this latter turned out to comprise two or more species. The figures in common brackets ( ) refer to the numbers in the list.

It is very understandable that HAECKEL, in his worship of beauty, was attracted by these pretty animals. His " System der Medusen ", followed immediately by his work on deep-sea medusae in the *Challenger* Reports (1881), is a mile-stone in the progress of our knowledge of the medusae, and this progress soon became rapid, especially when one great expedition after another was sent out to explore the oceans and their inhabitants. No wonder that the knowledge contained in HAECKEL'S works was soon considerably augmented, and the reliability of his apprehension of the observations, or even of the observations themselves, were considered open to doubt. In the present paper I hope to contribute to the removal of some of these cases of doubt.

When the next monograph of medusae appeared in A. G. MAYER'S " The Medusae of the World " (1910), H. B. BIGELOW had just published his outstanding work on the medusae of the eastern tropical Pacific (1909) to be followed (*provisionally* until 1940) by many other papers, to which the student of medusae must continually refer for valuable information.

ANTHOMEDUSAE

Codonium princeps Haeckel.

1879, p. 13, Pl. I, figs. 1, 2.

[*Sarsia princeps* (Haeckel).]

The description is based entirely on specimens in the Zoological Museum, Copenhagen. Specimens are still retained from the following localities:

(8 and 13) Greenland? Mus. zootom. Hafn. 3 specimens.

(9) Davis Strait and Baffin Bay; BORCH, 1859. 2 specimens.

(10) Greenland; 1865. 7 specimens.

(12) Umanak, Greenland; FLEISCHER, 1865 (Neotype). 1 specimen.

(137) Godhavn, Greenland; OLRIK, 1860. 12 specimens.

(138) Greenland. 4 specimens.

No. 22 in the list, Greenland, H. P. C. Möller, is determined by Haeckel as *Sarsia glacialis*; this specimen really belongs to *S. princeps*. Haeckel's statement of the colour of the species was based on sketches made by H. P. C. Möller. These sketches are in our museum and they were drawn partly at Frederikshaab in 1839, partly at Godthaab in 1840; they evidently represent *Sarsia tubulosa* and not *princeps*, showing no trace of an apical canal.

No. 11 in the list, taken north of the Faroe Islands by Steincke and identified by Haeckel as *Codonium princeps*, is unfortunately not in the collection. It is very improbable that this species should have been found in this southern locality.

Since no type-specimen was pointed out by Haeckel, I designate No. 12, Umanak, Fleischer, 1865, as *Neotype*.

Sarsia tubulosa

1879, p. 16.

Specimens identified by Haeckel as *Sarsia tubulosa* are retained from the following localities:

(15) Iceland; Steincke.
(16) Bordeyri, northern Iceland; Steincke. 2 specimens.
(17) Isafjord, Iceland; Mariboe, 1865. 2 specimens.
(18) Faroe Islands; Steenstrup, 1844. 2 specimens.

Steenstrupia galanthus

1879, p. 31.

[*Steenstrupia nutans* (M. Sars)]

No. 118 in the list, 49° N. 7° W., off the mouth of the English Channel, Hygom, 1857, is labelled by Haeckel *Steenstrupia* (*rubra* Forbes?). There are two specimens, belonging to *S. nutans*.

Stomotoca pterophylla Haeckel.

1879, p. 52, Pl. IV, fig. 10.

(168) 20° 36′ N. 76° W., north of Cuba; Andrea, 1867. 3 specimens, one of which I designate as *Neotype*.

Mayer (1910, p. 113) gives a new description of this species, slightly differing from that of Haeckel. Mayer presumes that certain errors in Haeckel's description are due to the state of preservation of the specimens. It is true that this may account for the absence of an apical projection and the finely serrate inner margin of the ring-canal. The so-called " Ocellarkolben " are rudimentary tentacle bulbs, and they have no ocelli; their number is as stated by Haeckel, and on the whole the description is in good accordance with the structure of the specimens.

Pandea saltatoria

1879, p. 54.

In the text of his monograph Haeckel only mentions the original specimen from Norway described by M. Sars (1835) as *Oceania saltatoria* (*Pandea saltatoria* Lesson 1843), a species which has never been identified with certainty, though Hartlaub (1913, p. 336) is inclined to think that it was an *Aglantha*.

In our collection is a specimen (No. 112 in the list) labelled by HAECKEL *Pandea saltatoria*, 14° N. 25° W., west of the Cape Verde Islands, collected by HYGOM in 1858. It belongs to *Pandea conica* Lesson. The number of exumbral nematocyst tracks corresponds to the number of tentacles.

Conis cyclophthalma Haeckel.

1879, p. 55, Pl. IV, fig. 1.

[*Oceania armata* Kölliker.]

(114) 36° 29′ N. 2° 28′ W., Mediterranean, near Gibraltar; BRANNER. (HAECKEL as the result of misprints gives the longitude as 2° 23′ W. and the name of the collector as BRAMER.)

This is the type specimen of *C. cyclophthalma*, and we are fortunate to have it in the collection. MAYER (1910, p. 130) retains the species within the genus *Conis* beside *C. mitrata* Brandt. HARTLAUB (1913, p. 342) has examined the type-specimen, and I can confirm his statement that it belongs to *Oceania armata* Kölliker. Thus *Conis cyclophthalma* is an obsolete name.

Oceania sp.

HAECKEL (1879, p. 56) declares that the generic name *Oceania* is obsolete, but in the list some medusae are mentioned as *Oceania* sp.? One of them, 28–33° N. 60–64° W., HEDEMANN, 1867, has disappeared, the others are in the collection and may be identified as follows:

(88) 21° S. 57° E., east of Madagascar; ANDREA, 1864, 2 specimens, 5 mm in height, with 8 tentacles; they belong to *Neoturris papua* (Lesson).

(126) 49° N. 7° W., off the mouth of the English Channel; HYGOM, 1857. 1 specimen, belonging to *Leuckartiara nobilis* Hartlaub.

Tiara pileata.

1879, p. 58.

(111) 36° 17′ N. 3° 27′ W. Mediterranean near Gibraltar; BRANNER, 1869. 4 specimens, labelled by HAECKEL: *Tiara pileata* = *Oceania* (*coccinea*). They belong to *Pandea conica* Lesson.

Tiara conifera Haeckel.

1879, p. 59.

(142 and 143) Greenland; OLRIK. 2 specimens.

HAECKEL'S description is entirely based on these specimens; they belong to *Catablema vesicarium* (A. Agassiz) as already presumed by HARTLAUB (1913, p. 315).

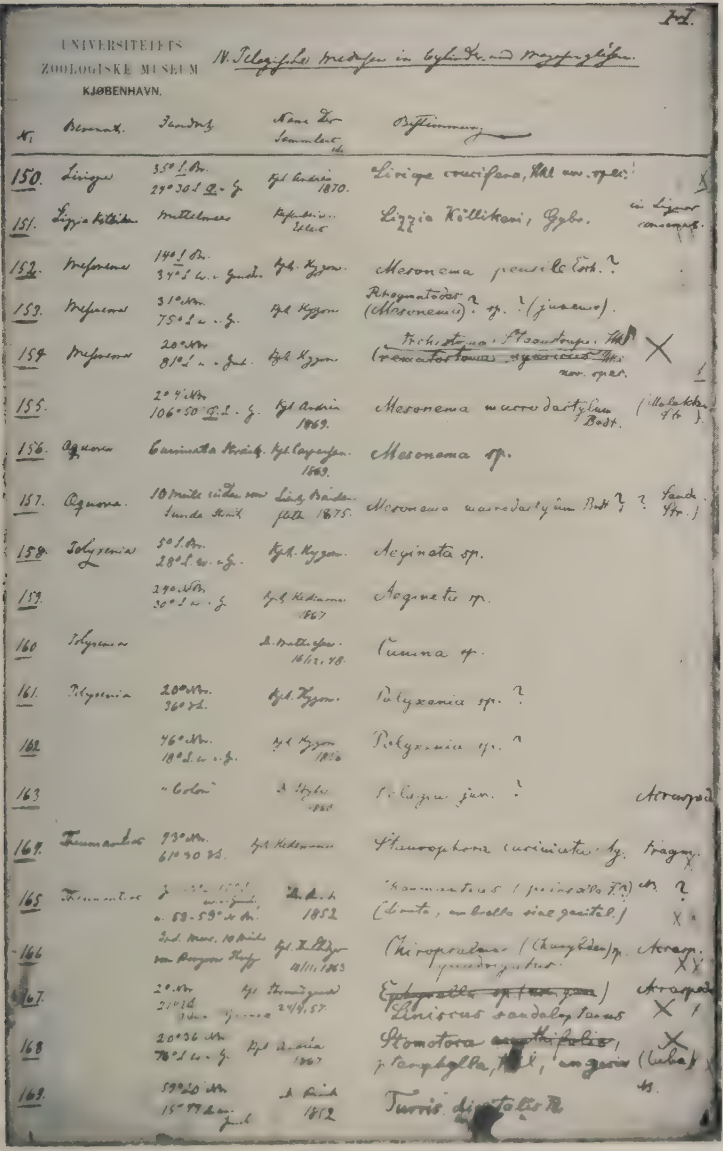
Tiara reticulata Haeckel.

1879, p. 60, Pl. III, fig. 11.

[*Pandea conica* Lesson.]

(104) 35° 31′ S. 0° 51′ W. Atlantic Ocean near Tristan da Cunha; ANDREA, 1862. 2 specimens.

These are the only specimens known, and they belong to *Pandea conica* Lesson, as already stated by HARTLAUB (1913, p. 340).



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KJØBENHAVN.

IV. Pelagische Medusen in Cylinder- und [illegible]

Nr.	Benennt.	Fundort	Name der Sammler etc.	Bestimmung	
150.	Liriope	35° S. Br. 24° 30' [illegible]	Kpt. Andrea 1870.	Liriope crucifera, Hkl nov. spec.!	
151.	Lizzia Köllikeri	Mittelmeer	[illegible]	Lizzia Köllikeri, Ggbr.	in Liquor conservat.
152.	Mesonema	14° S. Br. 34° [illegible]	Kpt. Hygom.	Mesonema pensile Esch.?	
153.	Mesonema	31° N. Br. 75° [illegible]	Kpt. Hygom	Rhegmatodes? (Mesonema)? sp.? (juven.).	
154	Mesonema	20° N. Br. 81° [illegible]	Kpt. Hygom	Trichostoma Steenstrupii Hkl ~~[illegible]~~ nov. spec.	×
155.		2° 4' N. Br. 106° 50' [illegible]	Kpt. Andrea 1869.	Mesonema macrodactylum Bndt.	(Malakka Str.)
156.	Aequorea	Carimata Strasse	[illegible] 1869.	Mesonema sp.	
157.	Aequorea.	10 Meile südlich von Sunda Strait	[illegible] 1875.	Mesonema macrodactylum Bndt? ?	Sunda Str.)
158.	Polyxenia	5° S. Br. 28° [illegible]	Kpt. Hygom.	Aeginata sp.	
159.		29° N. Br. 30° [illegible]	Kpt. Hedemann 1867	Aeginata sp.	
160	Polyxenia		[illegible] 16/12. 48.	Cunina sp.	
161.	Polyxenia	20° N. Br. 36° [illegible]	Kpt. Hygom.	Polyxenia sp.?	
162		46° N. Br. 18° [illegible]	Kpt. Hygom 1856	Polyxenia sp.?	
163		"Colon"	[illegible] 1866	[illegible] juv.?	Acraspeda
164.	Thaumantias	93° N. Br. 61° 30' [illegible]	Kpt. Hedemann	[illegible] sp.	fragm. ×
165	Thaumantias	[illegible] 58-59° [illegible]	[illegible] 1852	Thaumantias (pileata? F.?) [illegible] (diminuta, umbrella sine genital.)	? ×
166		[illegible] 10 Meile von Bergen [illegible]	[illegible] 18/11. 1863	Chiropsalmus (Chirodropus) sp. quadrigatus	Acrasp. × ×
167.		2° N. Br. 21° [illegible]	[illegible] 24/4. 57.	~~Ephyra [illegible] sp.~~) Linerges sandalophorus	Acraspeda ×
168		20° 36' N. Br. [illegible]	Kpt. Andrea 1867	Stomolophus ~~[illegible]~~, pterophylla, Hkl, [illegible]	× (Cuba)
169.		59° 20' N. Br. 15° [illegible]	[illegible] 1852	Turris digitalis [illegible]	

Fig. 1. Fascimile of one of the pages of the list of medusae sent from the Zoological Museum of Copenhagen to ERNST HAECKEL. The right half of the sheet contains the names of the species in HAECKEL's hand-writing.

Turris digitalis.

1879, p.61.

(44) 59° 20′ N. 15° 47′ W., between Scotland and Iceland; RINK, 1852. 7 specimens.

(47) 58–59° N., between Iceland and Greenland; RINK, 1852. 1 specimen.

(147) 59° 09′ N. 16° W., west of Scotland; OLRIK, 1861. 1 specimen.

These specimens were re-examined by HARTLAUB (1913, p. 329) and KRAMP (1926, p. 94). They belong to *Neoturris pileata* (Forskål).

Catablema campanula.

1879, p. 63, Pl. IV, figs. 4, 5.

[*Catablema vesicarium* (A. Agassiz).]

HAECKEL described this as a " nova species? ", indicating that it might be identical with *Medusa campanula* Fabricius, 1780. The description was based on the following specimens, which are still in our collection:

(43) Greenland; ZIMMER, 1856. 2 specimens.

(144) Umanak, Greenland; OLRIK, 1853. 7 specimens.

HAECKEL also referred to a coloured sketch by H. P. C. MÖLLER; the sketch is in our museum, and it was drawn after a specimen taken near Frederikshaab in Greenland in 1839; like the preserved specimens it undoubtedly belongs to *C. vesicarium.*

Catablema vesicarium.

1879, p. 64.

In his book HAECKEL only quotes the description of this species as given by A. AGASSIZ (1865) and says nothing about a specimen, which is in the collection, labelled by himself *Catablema vesicarium*:

(45) Greenland; MOBERG, 1857.

Catablema eurystoma Haeckel.

1879, p. 64, Pl. IV, figs. 6, 7.

The description of this species was based on specimens in the museum of Copenhagen and a coloured sketch by H. P. C. MÖLLER, drawn at Qajartalik in Arsuk Fjord in southern Greenland. The species is undoubtedly identical with *C. vesicarium* (A. Agassiz), but the specimens are lost. They were taken in the following locality:

(146) 67° 35′ N. 54° 10′ W., in South Strömfjord, Greenland; OLRIK, 1866.

Cytaeis nigritina Haeckel.

1879, p. 74, Pl. VI, figs. 2–5.

[*Cytaeis tetrastyla* Eschscholtz.]

On a previous occasion (KRAMP, 1953, p. 263) I have discussed the name of this species. HAECKEL applies the specific name *tetrastyla* only to the original form described by ESCHSCHOLTZ, but refers the numerous specimens from the museum of Copenhagen to a new species, *C. nigritina.* MAYER (1910, p. 133) tried to revive the name *atlantica* Steenstrup, 1837, but, as stated by me, this name was only found in STEENSTRUP's hand-written catalogue of the collection in our museum and was never published.

The specimens in our collection are derived from the following localities:

(72, 73) 14° N. 20° W., near Cape Verde Islands; PROSCH. 15 specimens, type specimens of *Cytaeis nigritina*.

(74) 8° 30′ N. 24° W., south of Cape Verde Islands; ANDREA, 1872. 2 specimens, labelled *Nigritina atlantica*.

(75) 31° 28′ N. 29° 39′ W., south of the Azores; ANDREA, 1860. 5 specimens, labelled *Nigritina* sp.

(76) 5° S. 28° W., off Cape San Roque, east coast of Brazil; HYGOM. 2 specimens, labelled *Nigritina* sp. (*polyblasta* ?).

(77) 23° 03′ N. 31° 48′ W., N.W. of Cape Verde Islands; MATHIESEN, 1848. 2 specimens, labelled *Nigritina atlantica*.

(78) 5° 31′ N. 23° 15′ W., south of Cape Verde Islands; REINHARDT. 1 specimen, labelled *Nigritina atlantica* (?).

(80) 34° N. 34° W., S.W. of the Azores; HYGOM. 1 specimen, labelled *Nigritina* (*polyblasta* ?).

(81) 6° N. 22° W., south of Cape Verde Islands; HYGOM. 3 specimens, labelled *Nigritina* (*polyblasta* ?).

(89) Atlantic Ocean; HYGOM, 1863. 1 specimen, labelled *Cytaeis nigritina*.

Before the publication of his book HAECKEL had evidently been much in doubt of the most convenient name of this species. The specific name *polyblasta*, applied to some of the specimens in the list, is found nowhere in the monograph; he may have thought about attaching this name to specimens carrying medusa buds.

Cytaeis macrogaster Haeckel.

1879, p. 74, Pl. VI, fig. 1.

[*Cytaeis tetrastyla* Eschscholtz.]

It is generally acknowledged that *C. macrogaster* is merely a synonym of *C. tetrastyla*, and an examination of the present specimens confirms this view.

(83) 0° S. 29° W., ANDREA, 1866. 2 specimens, designated as the types.

(84) 1° 20′ S. 26° 20′ W. ANDREA, 1863. 1 specimen.

(85) 2° 30′ N. 24° W. ANDREA, 1863. 4 specimens.

(87) 1° 30′ N. 24° W. ANDREA, 1863. 3 specimens.

All these localities are at a considerable distance N.E. of Cape San Roque on the east coast of Brazil.

Margelis principis Steenstrup.

1879, p. 88, Pl. VI, figs. 14–16.

The specimens labelled *Margelis principis* belong to two different species: *Bougainvillia principis* Steenstrup, and *B. superciliaris* L. Agassiz.

(3) Sandvaag, Faroe Islands; STEENSTRUP, 1844. The type-specimen of *Margelis principis*.

(5) Davis Strait off Holsteinsborg; OLRIK, 1859. 7 specimens.

(6) Godhavn, Greenland; OLRIK, 1860. 1 specimen.

The specimens from the two last mentioned localities are *Bougainvillia superciliaris*. No. 50 in the list, north of Orkney Islands, collected by OLRIK, 1859, is likewise identified by HAECKEL as *Margelis principis*, but the specimens are not in the collection.

Haeckel's figures of *Margelis principis* are said to be based on specimens from Iceland, but no Icelandic locality is mentioned in the list.

Hippocrene platygaster Haeckel.
1879, p. 91.
[*Bougainvillia platygaster* Haeckel.]

(107) 25° 04′ S. 27° 26′ W., S.W. of the islands of Trinidad; Andrea, 1869. 2 specimens, one of which I have designated as the type; by Haeckel himself named *H. platygaster* n.sp.

(110) 24° N. 33° W., about 700 miles N.W. of Cape Verde Islands; Iversen, 1871. 1 specimen, labelled *Margelis* (*platygaster*?).

In my report on the Hydromedusae of the *Discovery* expedition (in press), I have dealt with this species at some length. Numerous specimens were collected by the *Discovery* in the tropical parts of the Atlantic and off the east coast of Africa, and it was also taken by the *Dana* in some localities in West-Indian waters. In my opinion *Bougainvillia platygaster* is a valid species, distinct from *B. carolinensis* (McCrady), *B. fulva* Agassiz and Mayer, and *B. niobe* Mayer. I found that *B. platygaster* exhibits a most peculiar form of asexual propagation and, as a matter of fact, this same form of propagation is also observed in one of Haeckel's own specimens (No. 107), but it seems to have escaped his attention; at any rate, he does not mention it in his description.

Hippocrene superciliaris.
1879, p. 92.
[*Bougainvillia superciliaris* L. Agassiz.]

(1, 2 and 4) 66° 13′ N. 55° 05′ W., off South Strömfjord, Greenland; Moberg. 12 specimens.

These specimens really belong to *B. superciliaris*, as also some of the specimens erroneously identified as *B. principis* (see above).

Nemopsis heteronema Haeckel.
1879, p. 93, Pl. V, figs. 6–9.
[*Bougainvillia principis* Steenstrup.]

(7) Iceland; Steenstrup, 1839. 2 specimens.

Haeckel described these specimens together with some others from Norway collected by himself. As previously pointed out by me (Kramp, 1926, p. 48; 1939, p. 6) the specimens from Iceland belong to *Bougainvillia principis* (Steenstrup).

Rathkea fasciculata.
1879, p. 97.
[*Köllikerina fasciculata* (Péron & Lesueur).]

(151) Mediterranean; Keferstein and Ehlers.

In the list as well as on the label this specimen is named *Lizzia kölliikeri* Gegenbaur, but in the monograph the name is altered to *Rathkea fasciculata*.

LEPTOMEDUSAE

Thaumantias eschscholtzii Haeckel.

1879, p. 129, Pl. VIII, fig. 4.

[*Tiaropsis multicirrata* (M. Sars).]

(56) Greenland; HOLBÖLL, 1841. 1 specimen.

(58) Greenland, 1865. 2 specimens.

The description of this species was one of HAECKEL's great mistakes. The beautiful figure is reproduced in several handbooks as a typical " *Thaumantias* ", a leptomedusa, without any kind of marginal sense organs. As a matter of fact, it has eight large, black ocelli adjacent to eight large, open marginal vesicles.

When as a young man, in 1915, I commenced my work at the Zoological Museum of Copenhagen, I found the specimens mentioned above, and of course I was very interested to see the type specimens of the famous *Thaumantias eschscholtzii*, but while looking at them through an ordinary hand lens I saw eight black spots on their umbrella margin, and a closer examination revealed the fact that they belonged to the common and well-known *Tiaropsis multicirrata.* This surprising discovery was published by me in the reports of the Danish Ingolf-Expedition (KRAMP, 1919, p. 78; see also my revision of the Mitrocomidae, 1932, p. 364). To my regret " *Thaumantias eschscholtzii* " with a reproduction of the usual figure reappeared in KÜKENTHAL's " Handbuch der Zoologie ", Bd. I, 1924. The author of the article on Hydroida, my friend HJ. BROCH, Oslo, told me that his manuscript was delivered before 1914, and when the printing of the " Handbuch " was resumed after the war, he was not allowed to alter anything in his original text. Since then, however, I think that " *Thaumantias eschscholtzii* " has been regarded as an obsolete name.

Staurostoma laciniata.

1879, p. 130.

[*Staurophora mertensi* Brandt.]

(164) 43° N. 61° 30′ W., near Nova Scotia, Canada; HEDEMANN. Fragments of about 5 specimens.

The specimens were labelled *Staurostoma laciniata* Agassiz, and in the monograph it is placed among the Thaumantidae, whereas *Staurophora mertensi* Brandt, which is the same species, is mentioned (p. 149) under the Cannotidae.

Laodice cruciata.

1879, p. 132.

[*Laodicea undulata* Forbes & Goodsir.]

(53, 54) 59° 07′ N. 13° 32′ W., north of Rockall; MOBERG. 5 specimens, labelled *Laodice cruciata.*

(140) 59° N. 18′ W., between Iceland and Rockall; OLRIK. 3 specimens, labelled *Laodice cruciata.*

(165) 58–59° N. 13–15° W., north of Rockall; RINK, 1852. 5 specimens, labelled *Thaumantias* (*pilosella*?).

As demonstrated by BROWNE (1896, p. 482) there is only one single name among HAECKEL's 25 synonyms of " *Laodice cruciata* ", which really refers to a *Laodicea*, viz. " *Thaumantias mediterranea* " Gegenbaur (one of Haeckel's synonyms was

Thaumantias (*Cosmetira*) *pilosella* Forbes, which is a Mitrocomid). I have previously discussed the specific name (Kramp, 1919, p. 21) and adopted the name *undulata* Forbes & Goodsir, which was proposed by Browne (1907).

Orchistoma steenstrupii Haeckel.

1879, p. 139, Pl. XV, figs. 3–5.
[*Orchistoma pileus* (Lesson).]

(154) 20° N. 81° W., south of Cuba; Hygom. 3 specimens.

Two of the specimens are in good condition, and they agree quite well with the new description and figures by Mayer (1910, p. 211, Pl. 25, figs. 1–4), which were based on specimens from near the Bahamas and Tortugas. I agree with Mayer that *O. steenstrupii* is identical with *Mesonema pileus* Lesson (1843) and should be called *Orchistoma pileus*.

Ptychogena pinnulata Haeckel.

1879, p. 148; 1881, p. 7, Pl. II, figs. 1–8.
[*Ptychogena lactea* A. Agassiz.]

(139 and 141) 59° 07′ N. 13° 32′ W., between Ireland and Iceland; Moberg, 1857. 3 specimens, one of which is designated as the type.

As previously mentioned by me (Kramp, 1942, p. 55) this locality is most probably due to a mistake. This species is arctic, circum-polar, and it is hardly possible that it should occur so far to the south in the Atlantic. Haeckel's figures (1881) are remarkably beautiful and entirely correct.

Irene viridula.

1879, p. 202.

(60) Isafjord, north-western Iceland; Mariboe, 1865. 1 specimen.

In the list this specimen is identified as *Eirene* (*viridula*?). It really belongs to *Eutonina indicans* (Romanes), (see Kramp, 1919, p. 99).

Mesonema pensile.

1879, p. 226.

(156) Karimata Strait, west of Borneo; Caspersen, 1869. 1 specimen, diameter ca. 50 mm, about 125 radial canals and about 21 tentacles. Labelled *Mesonema* sp.

(152) 14° S. 34° W., off San Salvador, east coast of Brazil; Hygom. 3 specimens, with the following dimensions:

diam.	ca. 65 mm,	ca. 120	radial canals,	ca. 20 tentacles.
„	ca. 60 mm,	ca. 80	„ „	ca. 16 „
„	ca. 55 mm,	ca. 90	„ „	? „

The specimens No. 152 are determined in the list as *Mesonema pensile*? None of the localities are mentioned in the monograph.

In all the specimens the tentacle bulbs are provided with a distinct apical keel and spur; they undoubtedly belong to *Aequorea macrodactyla* (Brandt).

Mesonema macrodactylum Brandt.

1879, p. 226.

[*Aequorea macrodactyla* (Brandt)]

Besides the specimens mentioned above the collection contains one specimen of *Aequorea macrodactyla*, of which the label has been lost. It must have been derived from one of the following two localities, to which HAECKEL has added the determination *Mesonema macrodactylum*:

(155) 2° 04′ N. 106° 50′ E., near Singapore; ANDREA, 1869.

(157) 10 miles south of Sunda Strait; BARDENFLETH, 1875.

The specimen is about 50 mm in diameter, with about 125 radial canals and about 19 tentacles. None of these localities are mentioned in the monograph.

TRACHYMEDUSAE

Pectyllis arctica Haekel.

1879, p. 266.

[*Ptychogastria polaris* Allman.]

(148, 149) Pröven, about 72° 20′ N. on the west coast of Greenland; OLRIK, 1860. 5 specimens.

Besides these specimens HAECKEL examined a specimen taken near Halifax by the *Challenger* expedition in 1873. When he described the species, in 1879, he was not aware that in the previous year it had been described by ALLMAN as *Ptychogastria polaris*.

Aglantha digitalis.

1879, p. 272.

[*Aglantha digitale* (O. F. MÜLLER).]

In the list this species is recorded from numerous localities: specimens are still retained from the following:

(24) 58° 17′ N. 30° 59′ W. OLRIK, 1859. 6 specimens.

(30) 59° 07′ N. 13° 32′ W. MOBERG. 10 specimens.

(31) 57° 32′ N. 33° 31′ W. OLRIK, 1859. 5 specimens.

(32) Northern Atlantic Ocean; OLRIK, 1860. 6 specimens.

(35) 58–59° N., between Iceland and Greenland; RINK. 2 specimens.

(37) Ritenbenk, about 69° 40′ N. on the west coast of Greenland; ANDERSEN, 1862. 3 specimens.

(40) 58° 27′ N. 26° 43′ W. MOBERG, 1857. 4 specimens.

(41) 57° 48′ N. 43° 45′ W. OLRIK, 1861. 1 specimen.

(128) 57° 43′ N. 27° 03′ W. BANG, 1868. 8 specimens.

(130) Davis Strait, off Disco, about 69° N. OLRIK, 1862. 10 specimens.

(132) Godhavn, Disco, about 69° 12′ N. MOBERG, 1857. 1 specimen.

(134) Umanak, about 72° 40′ N., West Greenland; BROCKDORFF. 1 specimen.

HAECKEL altered O. F. MÜLLER's original spelling of the specific name *digitale* to *digitalis*.

HAECKEL has also added the name to two coloured sketches by H. P. C. MÖLLER, made at Fiskenässet and Godthaab in Greenland.

Liriope rosacea.

1879, p. 290.

[*Liriope tetraphylla* (Chamisso & Eysenhardt).]

The record of *L. rosacea* in the monograph is only a quotation from Eschscholtz (1829), who described it from near the equator in the Pacific Ocean as *Geryonia rosacea*; but in our collection are several specimens identified by Haeckel as *L. rosacea* from the following two localities:

(62, 63) 10° N. 105° E., in the Gulf of Siam; Strandgaard, 1860. 2 specimens.
(67) Red Sea; H. Koch, 1872. 6 specimens.

I agree with the authors who unite all the numerous " species " of *Liriope* into one: *L. tetraphylla* Chamisso & Eysenhardt.

Liriope crucifera Haeckel.

1879, p. 290.

[*Liriope tetraphylla* Chamisso & Eysenhardt.]

The description of this new species was based on the following specimen:

(150) 35° S. 24° 30′ E., near Algoa Bay on the south coast of Africa; Andrea, 1870. 1 specimen.

The description is in good accordance with the appearance of the specimen, but I see no reason for keeping the species distinct from *L. tetraphylla*.

Glossocodon lütkenii Haeckel.

1879, p. 293, Pl. XVIII, fig. 5.

[*Liriope tetraphylla* Chamisso & Eysenhardt.]

(65) 30° N. 17° W., north of the Canary Islands; Hygom, 1857. 1 specimen.
(66) 36–40° N. 26–45° W., west of the Azores; Andrea, 1861. 1 specimen.
(68) 35° N. 27° W., south of the Azores; Hygom, 1860. 1 specimen.

The new genus *Glossocodon*, of which this is the type-species, was said to differ from *Liriope* by the absence of interradial tentacles in the adult stage, whereas they are present in young specimens (like that from No. 68); evidently these tentacles were lost by preservation in the other specimens. The species *lütkeni* is further characterized by its very broad gonads, which have a peculiar distal incurvation, forming two lateral angular dilatations. There is no trace of this conformation of the gonads in the specimens Nos. 65 and 68, and in the specimen No. 66 it is distinct in only one of the four gonads. Accordingly there is no reason to retain *L. lütkeni* as a separate species.

NARCOMEDUSAE

Pegasia sieboldii Haeckel.

1879, p. 331.

This new species was described from a single specimen collected by Hygom in the tropical Atlantic. The specimen is not in our collection, and no " *Pegasia* " is mentioned in the list. According to Mayer (1910, p. 444) the species is probably identical with *Pegasia dodecagona* Péron & Lesueur; this is, however, a doubtful species. Haeckel's description seems to me to indicate that *Pegasia sieboldii* should be referred to *Pegantha triloba* Haeckel.

Genus *Pegantha* Haeckel.

In its modern sense the genus *Pegantha* comprises all the four genera, *Polycolpa*, *Polyxenia*, *Pegasia* and *Pegantha*, which in HAECKEL's monograph constitute the family Peganthidae. A considerable advance towards a revision of the numerous species of this group was made by H. B. BIGELOW in several papers, first and foremost in his beautiful work on the medusae collected in the eastern tropical Pacific by the S.S. *Albatross* in 1904 and 1905 (BIGELOW, 1909), in which adequate descriptions with pretty and elucidating figures are given of several species, in most cases based on his own examination of the specimens in life, or at least in the fresh condition. Valuable additions to our knowledge of these medusae are given in BIGELOW's subsequent papers, and by means of the extensive material collected by the *Discovery* expeditions I have recently been able to carry through an almost complete revision of the species belonging to *Pegantha* (to be published in the near future in the " *Discovery* Reports "). This has enabled me to identify the specimens previously examined by Haeckel. None of these specimens were, however, provided with definite specific, or even generic, names, as will be seen from the following notes, and none of the localities are recorded in HAECKEL's monograph.

There are four species of *Pegantha* in the collection; they are mentioned here under their proper names, as I have identified them, not according to the denominations given by HAECKEL in the list.

Pegantha martagon Haeckel.

Pegantha martagon Haeckel, 1879, p. 332.

(92) 29–31° N. 33–34° W. HYGOM. 3 specimens, determ. *Polyxenia*? sp.

(99) Atlantic Ocean north of the equator; WARMING, 1866. 1 specimen, determ. *Cunina* sp.

Pegantha triloba Haeckel.

Pegantha triloba Haeckel, 1879, p. 333.

(95) Atlantic Ocean south of the equator; FRIIS, 1861. 2 specimens, determ. *Aegineta*?

Pegantha laevis H. B. Bigelow.

Pegantha laevis H. B. Bigelow, 1909, p. 97, Pl. 16, fig. 1, Pl. 20, figs. 4–6, Pl. 27, figs. 1–7.

(90) 20° N. 40° W., between Africa and the West-Indies; HYGOM, 1860. 2 specimens, determ. *Cunina*? sp.

(94) 22° N. 22° W., between the Canary Islands and the Cape Verde Islands; HYGOM. 1 specimen, determ. *Aegineta* sp.

(97) 25° 05′ N. 30° W., N.W. of the Cape Verde Islands; R. NIELSEN, 1868–69. 2 specimens, determ. *Polyxenia*? sp.

(98) No locality given; MATHIASEN. 1 specimen, determ. *Polyxenia* sp.

(115) West-Indies; SUENSSON. 1 specimen, determ. *Cunina*? sp.

(160) 8° 38′ N. 24° 58′ W., S.W. of the Cape Verde Islands; MATHIASEN, 1848. 4 specimens, determ. *Cunina* sp.

Pegantha clara R. P. Bigelow.
Pegantha clara R. P. BIGELOW, 1909, p. 80, 2 figs.
Pegantha smaragdina H. B. BIGELOW, 1909, p. 90, Pl. 14, figs. 1–2, Pl. 19, figs. 1–9, Pl. 22–26.

(93) 3° S. 27° W., N.E. of Cape San Roque, Brazil; HYGOM. 1 young specimen, determ. *Polyxenia*? sp.

Aeginopsis laurentii Brandt.
1879, p. 342.

(145) Greenland; HOLBÖLL, 1841. 3 specimens.

HAECKEL has only determined these specimens as *Aegina* sp.?, and they are not mentioned in the monograph. They belong to the high-arctic species *Aeginopsis laurentii* Brandt, 1838.

SCYPHOMEDUSAE

In the collection of the Zoological Museum of Copenhagen are several ancient specimens of Stauromedusae, mainly identified by J. STEENSTRUP. They were not sent to HAECKEL, and the localities where they had been taken are not mentioned in his monograph. They will therefore not be mentioned here.

Some of the specimens belonging to other groups of Scyphomedusae and examined by HAECKEL have been re-examined and correctly identified by G. STIASNY, Leiden, whereas I am responsible for the revision of the others.

Periphylla hyacinthina.
1880, p. 419, Pl. XXIV.
[*Periphylla periphylla* (Péron & Lesueur).]

The collection contains several specimens of this species; all of them had previously been labelled as *Charybdea hyacinthina* by STEENSTRUP who had, however, never published any account of them. In the list as well as in his monograph HAECKEL has altered the name to *Periphylla hyacinthina* Steenstrup, and since the time of HAECKEL this name has usually been accepted. On a previous occasion (KRAMP, 1947, pp. 40 ff) I have discussed the generic as well as the specific name of this medusa. I retained the generic name *Periphylla*, but I came to the conclusion that the specific name *hyacinthina* had to be altered, because STEENSTRUP, who applied it to his specimens, never published it but merely wrote it on the labels of the specimens and in the hand-written journals of the museum, the " Acta Mus. Hafniensis " 1837 and 1842, which are quoted by HAECKEL. As a specific name *hyacinthina* was first used for this species by LÜTKEN (1875) and then by HAECKEL (1879), but the species had been described several times before under different names (for details, see KRAMP, 1947), and to avoid further confusion I stuck to the first indubitable name, *periphylla* Péron & Lesueur, 1809. In my opinion the correct name of this medusa must be *Periphylla periphylla* (Péron & Lesueur).

With one insignificant exception (Greenland, without further particulars, 1842) the specimens determined by HAECKEL are all in our collection, and since the localities have not previously been published in details, it may be desirable to give them here.

(202, 203, 205, 210, 213) Greenland; MÖLLER, JÖRGENSEN a.o. 8 specimens.
(206) Godthaab, Greenland; BLOCH, 1845. 1 specimen.
(207) 57° 28′ N. 41° W. OLRIK, 1864. 1 specimen.
(208) 43° N. 23° W., north of the Azores; HYGOM, 1857. 1 specimen.
(209) 57° 27′ N. 35° W. OLRIK, 1864. 1 specimen.
(211) 57° 40′–57° 27′ N. 35–39° W. OLRIK, 1862 and 1864. 2 specimens.
(212) Davis Strait; BORCH, 1859. 2 specimens.
(214) 48° N. 8° W., Bay of Biscay; HYGOM, 1851. 1 specimen.
(215) 39° N. 13° W., off Lisboa, Portugal; HYGOM, 1863; 1 specimen.
(217) 46° N. 18° W., off the Bay of Biscay; HYGOM, 1856. 1 specimen.
(227) 57° 49′ N. 35° 24′ W. BANG, 1868. 1 specimen.
(228) S.E. of Cape Farewell; BORCH, 1859. 3 specimens.
(229) 60° 12′ N. 52° 15′ W. OLRIK, 1864. 1 specimen.
(230) 66° 13′ N. 55° 05′ W. MOBERG. 1 specimen.

With the exception of Nos. 208, 214, 215 and 217 these localities are in the surroundings of the southern parts of Greenland.

Moreover, HAECKEL has applied the name *Periphylla hyacinthina* to coloured sketches by H. P. C. MÖLLER from the following localities: 60° 19′ N. 17° W., 58° N. 28° W., 57° 12′ N. 53° 58′ W., and Julianehaab in Greenland, 1838–1840.

Charybdea marsupialis.
1880, p. 442.
[*Carybdea marsupialis* (Linné).]

(201) Harbour of Malaga, Mediterranean coast of Spain; HYGOM, 1853. 3 specimens.
(216) During a journey to the West-Indies; SUENSSON. 1 specimen.

Chiropsalmus quadrigatus Haeckel.
1880, p. 447.

(166) Indian Ocean off Rangoon; THALBITZER, 1863. 1 specimen.

This is the type specimen; it was re-examined by STIASNY (1922 A, p. 517), who retains the species in spite of its bad condition and refers a second specimen, collected in Johore Strait, 1901–02, to the same species.

Linerges pegasus Haeckel.
1880, p. 495.
[*Linuche unguiculata* (Schwartz, 1788) Eschscholtz, 1829.]

(105) West-Indies, or on journey to the West-Indies; SUENSSON. 5 specimens.

The description of this species was based partly on specimens from Campeche Bay in the Gulf of Mexico, partly on the present specimens. These latter evidently belong to the widely distributed species *Linuche unguiculata* (Schwartz).

Linerges mercurius Haeckel.
1880, p. 495, Pl. XXIX, figs. 4–6.
[*Linuche unguiculata* (Schwartz).]

(101) 19° 54′ N. 81° 45′ W., south of Cuba; CASPERSEN, 1870. 1 specimen.
(102) 20° 20′ N. 73° W., between Cuba and Haiti; ANDREA, 1861. 1 specimen.

This species is undoubtedly identical with *Linuche unguiculata*; at least the present specimens certainly belong to that species.

Linerges draco Haeckel.
1880, p. 496.

(100) 5° N. 107° E., China Sea; CASPERSEN, 1869. 1 specimen.

HAECKEL by a misprint gives the longitude as 107° *W.* in the China Sea. This is the type specimen. Later on the species has been recorded from the Malayan Archipelago (MAAS, 1903, p. 24) and New Britain (Neu Pommern) N.E. of New Guinea (THIEL, 1927, p. 27). I think we should follow THIEL in regarding it as a valid species.

Liniscus sandalopterus Haeckel.
1880, p. 497.
[*Linuche unguiculata* (Schwartz).]

(167) 2° N. 21° W., off Sierra Leone, West Africa; STRANDGAARD, 1857. 4 specimens.

In his monograph HAECKEL also records this species from the tropical part of the Atlantic collected by KÔCH and HEDEMANN, but in the list these specimens are determined as *Liniscus cyamopterus* (see below). *Liniscus sandalopterus* has not been observed, since it was described by HAECKEL, and the specimens evidently belong to *Linuche unguiculata. L. sandalopterus* accordingly is an obsolete name.

Liniscus cyamopterus Haeckel.
1880, p. 497.
[*Nausithoë punctata* Kölliker.]

(103) Atlantic Ocean, without particulars; KOCH, 1860. 1 specimen.
(106) Atlantic Ocean; HEDEMANN. 3 specimens.

The specimens are labelled *L. cyamopterus*, and they are provided with the same name in the list; they are, however, large specimens of *Nausithoë punctata* Kölliker.

Pelagia perla.
1880, p. 506.
[*Pelagia noctiluca* (Forskål).]

(177) Northern Atlantic; OLRIK, 1860. 3 specimens.

Pelagia perla is identical with *P. noctiluca.*

Pelagia phosphora Haeckel.
1880, p. 506.
[*Pelagia noctiluca* (Forskål).]

(170 and 231) 7° N. 22° W. HYGOM, 1850. 3 specimens.
(171) 8° 38′ N. 24° 58′ W. MATHIASEN. 1 specimen.
(172) 36° N. 41° W. *Galathea*, 1842. 3 specimens.
(175) 7–13° N. 57° W. HYGOM. 6 specimens.
(174) Atlantic Ocean; HYGOM. 2 specimens.
(178) 11° N. 22° W. HYGOM, 1853. 1 specimen.
(180) Cape Verde Current; PROSCH. 4 specimens.
(225) 14° N. 20° W. PROSCH.

HAECKEL has referred all these specimens to his new species *Pelagia phosphora*, which, however, cannot be kept apart from *P. noctiluca* (Forskål).

A young specimen, labelled *Pelagia* juv., No. 116 in the list, taken in the Bay of Biscay, 47° N. 7° 30′ W., likewise belongs to *P. noctiluca.*

Pelagia cyanella Péron & Lesueur.
1880, p. 507.
[*Pelagia noctiluca* (Forskål).]

(176) No locality stated. *Galathea* exped. 1 specimen, determined *P. cyanella*?

Stenoptycha dactylometra Haeckel.
1880, p. 526.
Cyanea capillata (L.).

This species is not in the list, and no specimen is preserved, but the coloured drawing by H. P. C. MÖLLER, mentioned by HAECKEL in his monograph, is in our possession. It evidently represents a young *Cyanea capillata* with only 5 tentacles in each of the eight groups.

Cyanea arctica Péron & Lesueur.
1880, p. 530.
[*Cyanea capillata* (L.).]

(183) Davis Strait; OLRIK, 1866. 2 specimens.

(220) Greenland; HOLBÖLL, 1841. 1 specimen.

HAECKEL determined these specimens as *Cyanea arctica*. As previously demonstrated by me (KRAMP, 1942, pp. 128 ff) the common *Cyanea* occurring in the Greenland waters and along the east coast of North America differs in no way from the European *C. capillata*.

Aurelia flavidula Péron & Lesueur.
1880, p. 555.
[*Aurelia limbata* Brandt.]

(181) Davis Strait; OLRIK, 1866. 5 specimens.

The complicated history of the Greenland and East-American forms of *Aurelia* was thoroughly dealt with by me in a previous paper (KRAMP, 1942, pp. 109 ff), to which I refer, especially concerning the discussion (p. 122) of the specific names of the two species. The present specimens belong to the yellow form with complexly branching and anastomosing canals described from the northern Pacific by BRANDT (1838) as *Aurelia limbata*. It was probably the same species, which was observed at Greenland by O. FABRICIUS (1780), and it was to this that PÉRON and LESUEUR applied the name *A. flavidula*. Unfortunately, L. AGASSIZ accepted this name for the common American *Aurelia* which, however, belongs to the same species as the European *A. aurita* (L.), though the American form differs somewhat from the European and should be designated as a distinct variety, *A. aurita* var. *occidentalis* (KRAMP, 1942, p. 125).

This variety of *A. aurita* also occurs along the southern part of the west coast of Greenland; it is not mentioned in HAECKEL's list, but to a drawing by H. P. C. MÖLLER of a six-rayed specimen (locality not stated) HAECKEL has added the name *Aurelia flavidula* var. *sex radiis*. Another drawing by MÖLLER (Frederikshaab, 1839) apparently represents *A. limbata*.

Polyclonia frondosa.
1880, p. 568.
[*Cassiopea frondosa* (Pallas).]

(187 and 188) West-Indies; Nat. Hist. Mus. Copenhagen. 2 specimens.
(189) St. Croix, West-Indies; ÖRSTED and RAVN, 1836. 3 specimens.
(190) West-Indies; SUENSSON. 1 specimen.

Polyrhiza vesiculosa.
1880, p. 577.
[*Netrostoma coerulescens* Maas.]

(185) Gulf of Suez, Red Sea; KOCH, 1872. 1 specimen.

The specimen is mentioned by HAECKEL in his monograph. It was re-examined by STIASNY (1922 A, p. 527), who found that this specimen most probably belongs to *Netrostoma coerulescens* Maas, and I think he was right in this respect.

Stomolophus fritillaria Haeckel.
1880, p. 598, Pl. XXXV.
[*Stomolophus meleagris* L. Agassiz, var. *fritillaria.*]

(195, 196, 197) Surinam, on the northern Atlantic coast of South America; Mus. zootom. Hafn. 3 specimens.

Haeckel's description and beautiful figures of this species were based on these specimens.

In our collection is a fourth specimen (No. 198 in the list) of unknown origin, likewise identified by HAECKEL as *S. fritillaria.* The locality where it was taken is given as 43° N. 61° 30′ W., i.e. near Nova Scotia! The specimen is in an excellent condition, and there is no doubt of the correctness of the identification, but it seems impossible that any of the two species of *Stomolophus* might occur so far to the north; the distribution of both species is decidedly tropical. Evidently the note of the locality, in the label as well as in the list, must be due to some error.

There is no doubt that *Stomolophus agaricus* Haeckel (see below) is identical with *S. meleagris* Agassiz, and *S. chunii* Vanhöffen belongs either to *meleagris* or to *fritillaria*, but the relation between these two latter species has been much discussed.

MAYER (1910, p. 711) regards *S. fritillaria* as a southern variety of *S. meleagris.* " The only valid distinction between this medusa and *S. meleagris* are in its large number of marginal lappets, and in the cleft in the middle of each octant of velar lappets. Also the 16 scapulets are hidden well up under the bell instead of extending down to about the level of the bell margin." Moreover, *S. fritillaria* does not seem to grow to a larger size than 80 mm in diameter, whereas *meleagris* may attain a diameter of 120 mm. BIGELOW (1914, pp. 239–241) likewise unites the two species. STIASNY, however, who examined several specimens from Dutch and British Guiana and Trinidad (STIASNY, 1922 B, pp. 55–59; 1931, pp. 169–175) recognizes *S. fritillaria* as a valid species, though in the latter of these papers he points out so much variability in both forms that he admits that BIGELOW may be right. Unfortunately, STIASNY had not seen the original specimens in Copenhagen; he even states in a footnote (1922, p. 55) that they had disappeared; fortunately, they have been rediscovered in our collection, so I have been able to examine them. BIGELOW (1940, p. 316) once more discussed the question of the two species and concluded that " the union of *meleagris* and *fritillaria* may . . . be allowed to stand, at least provisionally ". On the other hand, RANSON (1949, pp. 150–154) through a careful examination of specimens from French Guiana and others from the Gulf of California and Ecuador, once more separated the two forms, pointing out several distinguishing features, especially that in *fritillaria* the scapulets are " plus profondement situées dans la sous-ombrelle ".

This latter feature, which was emphasized by MAYER as well as by HAECKEL himself, is very distinct in all the original specimens and really seems to be characteristic of *fritillaria*. On the other hand, I can see no indication of the median incurvations of the umbrella margin between the rhopalia, described and figured by HAECKEL. It is difficult to state the exact number of marginal lappets in the original specimens, but as far as I can see, the number of velar lappets does not exceed 12 or 16 in each octant; each lappet is, however, divided into two by a short median line; this was also observed by RANSON in the specimens from Trinidad examined by him

The specimen labelled 43° N. 61° 30′ W. is particularly well preserved and about 60 mm in diameter. One of the three specimens from Surinam is about 50 mm wide and rather badly preserved; another of these specimens is about 80 mm wide and somewhat torn. The largest specimen, from which presumably HAECKEL'S figure of the entire medusa was drawn, and which may be designated as the type, has been cut into several pieces.

It seems to me that the differences between *S. fritillaria* and *meleagris* are so slight that they do not justify a distinction of two separate species, but sufficient to regard *fritillaria* as a distinct variety of *meleagris*; so I am inclined to adhere to the views of MAYER and BIGELOW.

Stomolophus agaricus Haeckel.

1880, p. 597.

[*Stomolophus meleagris* L. Agassiz.]

(199) Punta Arenas, Pacific coast of Costa Rica, Central America; ÖRSTED, 1843. 1 specimen.

According to STIASNY (1922 A, p. 553), who has examined the specimen, it may be regarded as belonging to *S. meleagris* L. Agassiz, as already presumed by MAYER (1910, p. 710).

Versura palmata Haeckel.

1880, p. 606, Pl. XL, figs. 9-12.

[*Mastigias ocellata* (Modeer).]

(186) Cheribon, north coast of Java; ANDREA, 1870. 1 specimen.

By a careful examination of the present type-specimen STIASNY (1922 A, p. 538) referred it to *Mastigias ocellata* (Modeer).

Cotylorhiza tuberculata (Macri).

1880, p. 610.

(200) Trieste, Adriatic Sea; STEENSTRUP. 1 specimen. Correctly identified.

Cotylorhiza? (*Stylorhiza*?).

[*Mastigias ocellata* (Modeer).]

(194) 1° N. 104° E., near Singapore; STRANDGAARD. 1 specimen.

STIASNY (1922 A, p. 530) has identified this specimen as *Mastigias ocellata* (Modeer).

Mastigias papua (Lesson).

1880, p. 623.

(191) China Sea, East Asia; Koch, 1872. 1 specimen.

This locality is mentioned in Haeckel's monograph, and the identification is undoubtedly correct.

No. 192 in the list is a fragment collected by Strandgaard, 4° S. 106° E. Haeckel denominated it " Rhizostomae fragmentum ". Stiasny (1922 a, p. 529) refers it to *Mastigias papua* (Lesson).

Cramborhiza flagellata Haeckel.

1880, p. 646.

[*Lychnorhiza lucerna* Haeckel.]

(193) Cotinguiba, Brazil; Hygom. 1 specimen.

Haeckel mentions this specimen in his monograph as well as in the list as *Cramborhiza flagellata*, together with a specimen from Pernambuco. Mayer (1910, p. 673) regards it as a young stage of *Lychnorhiza lucerna* Haeckel, and Stiasny (1922 c, p. 235) agrees with Mayer in this respect. An examination of the present specimen does not contradict this view. It is in a fairly good condition, about 55 mm wide, and immature. The oral arms are slightly longer than the radius of the umbrella; some few filaments are present, and they are very short. Between two successive radial canals there is usually only one centripetal canal issuing from the ring-canal, but sometimes two, one of which is small.

REFERENCES

Agassiz, A. (1865), North American Acalephae. 234 pp.

Bigelow, H. B. (1909), *Reports of the scientific results of the Expedition to the Eastern Tropical Pacific*, 1904–1905. XVI. The Medusae. *Mem. Mus. Comp. Zool., Harvard Coll.*, **37**, 243 pp.

Bigelow, H. B. (1914), Note on the medusan Genus *Stomolophus*, from San Diego. *Univ. California Publ., Zool.*, **13** (10), 239–241.

Bigelow, H. B. (1940), Medusae of the Templeton Crocker and Eastern Pacific *Zaca* Expeditions, 1936–1938. *Zoologica, N.Y. Zool. Soc.*, **25** (3), 281–321.

Bigelow, R. P. (1909), A new Narcomedusa from the North Atlantic. *Biol. Bull.*, **16**, 80–82.

Brandt, J. F. (1838), Ausführliche Beschreibung der von C. H. Mertens auf seiner Weltumsegelung beobachteten Schirmquallen. *Mém. Acad. Imp. Sci., St. Pétersbourg*, (6), **4** (2), 237–411.

Browne, E. T. (1896), On British Hydroids and Medusae. *Proc. Zool. Soc., London*, 459–500.

Browne, E. T. (1907), A revision of the Medusae belonging to the Family Laodiceidae. *Ann. Mag. Nat. Hist.* (7), **20**, 457–480.

Eschscholtz, Fr. (1829), *System der Acalephen* - - -. Ferdinand Dümmler, Berlin, 188 pp.

Fabricius, O. (1780), *Fauna Groenlandica.* Hauniae et Lipsiae, 452 pp.

Haeckel, E. (1879–80), Das System der Medusen. *Jena Denkschr. Med.-Natur.-wiss. Gesell.*, **1** (1, 2), 1–672.

Haeckel, E. (1881), Report on the deep sea Medusae. *Rept. Sci. Res., H.M.S.* Challenger, *Zool.*, **4**, 154 pp.

Hartlaub, Cl. (1913–17), Craspedote Medusen. *Nordisches Plankton*, **12** (1), 237–379.

Kramp, P. L. (1919), Medusae I. Leptomedusae. *Danish Ingolf Exped.*, **5** (8), 111 pp.

Kramp, P. L. (1926), Medusae II. Anthomedusae. *Danish Ingolf Exped.*, **5** (10), 102 pp.

Kramp, P. L. (1932), A revision of the Medusae belonging to the Family Mitrocomidae. *Vidensk. Meddel. Dansk Naturhist. Foren.*, **92**, 305–383.

Kramp, P. L. (1939), Medusae, Siphonophora, and Ctenophora. *Zool. of Iceland*, **2** (5b), 1–37.

Kramp, P. L. (1942), Medusae. " Godthaab " Expedition, 1928. *Meddel. om Grönland*, **81** (1), 1–168.

Kramp, P. L. (1947), Medusae III. Trachylina and Scyphozoa, with zoogeographical remarks on all the Medusae of the Northern Atlantic. *Danish Ingolf Exped.*, **5** (14), 66 pp.

Kramp, P. L. (1953), Hydromedusae. *Great Barrier Reef Exped.*, 1928–29, *Sci. Repts.*, **6** (4), 259–322.

Lütken, Chr. (1875), A revised list of the Acalephae and Hydrozoa of Greenland. Arctic Manual and Instructions. Copenhagen. 187–190

Maas, O. (1903), Die Scyphomedusen der Siboga-Expedition. *Siboga-Exped., Monogr.*, 11, 91 pp.

Mayer, A. G. (1910), Medusae of the world. (3 vols.) *Carnegie Inst., Washington, Publ.*, No. 109 735 pp.

Ranson, G. (1949), Méduses. Résultats scientifiques des croisières Navire-École Belge " Mercator " 4 (2). *Mém. Inst. Roy. Sci. Nat. de Belgique*, (2), 33, 121–158.

Stiasny, G. (1922 a), Die Scyphomedusen-Sammlung von Dr. Th. Mortensen nebst anderen Medusen aus dem zoologischen Museum der Universität in Kopenhagen. *Vidensk. Meddel. Dansk Naturhist. Foren.*, **73**, 513–558.

Stiasny, G. (1922 b), Ergebnisse der Nachuntersuchung einiger Rhizostomeen-Typen Haeckel's und Schultze's aus der Sammlung des Zoologischen Institutes der Universität in Jena. *Zool. Mededeel., Leiden*, **7** (1–2), 61–79.

Stiasny, G. (1922 c), Ergebnisse der Nachuntersuchung einiger Rhizostomeen-Typen Ehrenberg's, Haeckel's und Vanhöffen's aus den Zoologischen Museen in Berlin und Königsberg. *Zool. Mededeel., Leiden*, **7** (3–4), 225–241.

Stiasny, G. (1931), Die Rhizostomeen-Sammlung des British Museum (Natural History) in London. *Zool. Mededeel., Leiden.*, **14** (3), 137–178.

Thiel, M. E. (1927), Die Scyphomedusen des Zoologischen Staatsinstituts und Zoologischen Museums in Hamburg. I. Cubomedusae, Stauromedusae und Coronatae. *Mitt. Zool. Staatsinst. u. Zool. Mus., Hamburg*, **43**, 1–34.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 169-177.

Some very simple devices for various oceanographical uses

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Summary—An account is given of some very simple ways of determining the underwater courses of suspension and towing lines in respect both of slope and direction. The means employed is to enclose pendulums and compasses within suitable vessels containing hot gelatine solution. These are affixed to the lines whilst the gelatine solution is hot, so that after the cooling which comes from immersion in the sea, the pendulums and compasses become immovably fixed to give the necessary records. It is shown that the devices could serve very usefully in studies of the pelagic trawl, and could be adapted to determine the shape of trawling cables leading all the way down into the greatest ocean depths.

IT WILL be of assistance if brief reference is made at the outset to two recently published papers. In one of them (CARRUTHERS, 195 4A, 181 *et seq.*) a preliminary account was given of a simple current-measuring instrument designed for use by commerical fishermen at echo-dictated depths. With that instrument, the speed and heading of the water movement are given by the amount and direction of tilt imposed by the current upon a cone made of non-magnetic mesh metal which is hung near its apex in a smooth roller bearing carried in a sort of tuning-fork bracket. The latter is borne on and can swing freely all round a rope strained between an anchor and a buoy well below surface. To the latter is attached (for recovery) a long length of strong thin line bent to a little marker buoy which serves as a finder—the whole system being cast freely into the sea without any need for the investigating ship to anchor. The bracket holds the cone well away from the line on which it is worked.

Though, in the definitive model, the record for slope and direction is given by the operation of a simple mechanism which locks a pendulum containing a compass within itself, in an earlier model the record was got as follows:

Rigidly fastened within the cone was a wide-necked bottle made of heat-resisting glass filled half with gelatine solution and half with common kerosene. After a brief sojourn of the bottle in the sea subsequent to its having first been stood in a bucket of hot water, the gelatine solution solidifies beneath the kerosene—the slant of the firm interface then formed being that imposed on the cone by the current. The slope is easily measurable after recovery, and is of course convertible into a speed value on reference to a calibration table.

It was additionally useful to arrange for a small ring compass of aircraft type to " float " at the interface of the two hot liquids. This was easily done by affixing a diminutive buoy above the compass to the end that, when congelation took place, the direction of the tilt was preserved. The arrangement can be appreciated from the appropriate illustration which shows such a compass floating unrestrained between the two hot liquids in a glass jug (Fig. 1). In use, the bottle is of course closed by means of a cork or a screw-on metal cap made of aluminium or copper.

In what follows attention will be paid to other uses of the simple device just described which will be referred to for brevity and convenience as a " jelly bottle ".

In the other paper (CARRUTHERS, 1954 B) an account was given of a directional wire-angle gauge designed for use on the hydrographical wire which carries the water bottles used for the routine collection of water samples and temperature data. The gauge is messenger-operated and is usable intermediately with the bottles. From it one learns the actual slope of the wire both in magnitude and direction so long as the wire is sufficiently weighted ($\nless$200 lbs) to preclude the heavy pendulous gauges from introducing local deformations into the wire because of their own weight.

We shall describe a simple method of checking the showings of such gauges—a method which could be extended to determine the underwater course of a deep-sea trawling cable leading all the way down into the greatest ocean depths. Then, it would be possible to learn the amount and direction of slope at discrete intervals all the way down such a cable as was used by Bruun from the *Galathea* when bottom-dredging in the Philippines Trench, in keeping with Kullenberg's calculations.

It should be remarked that when describing the earliest versions of the current-measuring cone above referred to, a description was added of how both direction and slope could be determined from a compass poised in hot gelatine only — without need to use the kerosene as well (CARRUTHERS, 1954 A, p. 185).

We are particularly interested to detail simple ways of determining the underwater course of lines, wires, ropes or warps let down from stopped vessels occupied with the activities of routine oceanographical stations, or towed behind ships engaged in trawling or analogous operations. Clearly, if jelly bottles of the kind described were suitably affixed to such lines, their simple round shape would be a great boon because it would not matter how they were disposed on the wire (above, below, or laterally) so long as parallelism were maintained.

It is not overlooked that a jelly bottle whose gelatine will remain uncongealed long enough to permit slope determinations to be made of hydrowires, may have too short a liquid life to be usable for investigating the underwater course (slope and direction) of the warps on which a pelagic trawl is towed, but it will be an easy-enough matter to achieve longer timings by using greater bulks of hot jelly in bigger bottles, or by encasing the jelly bottles in suitable covers to be filled with hot water before immersion in the sea. Whatever be the form of slope indicator decided upon, neutral buoyancy will be approximated to guard against the production of local deformations in the line.

This is a matter of importance because of the great interest which attaches to deciding the fishing depth of an off-bottom trawl.

It is believed that the simple devices here being considered could be profitably used to find at what depth a pelagic trawl had fished, at what height above bottom its foot-rope had ridden, what had been the distribution of its vertical gape and of its horizontal gape.

We have here no concern at all with the very ingenious instruments which use electronics and acoustics to telemeter net depth back to the towing ship whilst the tow is in progress, but fully appreciate the value to a fishing skipper of always knowing at what depth his pelagic net is fishing, so that he can alter his speed or warp length to keep it at the depth where his echo sounder tells him the fish are.

Because it seems quite unlikely that ordinary fishing craft will ever carry the telemetering net-depth indicators now being tested, it has seemed well worth while to line up with opinion that a necessary pre-requisite to achieving anything simpler which can be relied upon, is to determine the exact underwater course of the towing warps all the way from ship to net.

Though insufficiently acquainted with the latest achievements of Dr. J. SCHÄRFE of the Net Research Institute at Hamburg, who has carried out some very interesting investigations of the pelagic trawl with the aid of instruments specially developed for the purpose (SCHÄRFE, 1953), the writer knows of no such determination ever having been made as yet, but there seems no real need for the complexities of a recording instrument which would travel all the way along the warps to effect it. It seems amply good enough to measure the slope of a warp at a lot of discrete points where slope alone is the matter of interest, and to measure slope *and* direction at many points along the two warps where both slope and separation (roughly telling net gape) are wanted.

It could well be that, after learning the average slope of the whole warp lengths for different speeds of tow and various lengths of warp veered (which average slope would reveal fishing depth), it might be found possible to apply " corrections " to the readings of the deck inclinometer used to measure the entry angle of the warps. It is worth hoping that such " corrections " could become known for all lengths of warp out and all towing speeds so that the easily observed entry angles could be converted into approximate mean slope values and a table of implied net depths consulted with confidence.

WARP SLOPE

Where only one cable towed astern is being investigated, the rectangular instrument pictured (Fig. 2A and 2B) is a suitable and convenient one to use. It is a slender box of about cigar-box size and shape with front and back of clear perspex and is filled with gelatine solution only. Inside is a pendulum which can move freely so long as the gelatine solution remains liquid after prior immersion of the instrument in a bath of hot water. It is intentionally not fitted to the warp or towing rope by clamps, but through the medium of the bracket shown, which is secured on the warp, thin wire, or rope, by winding round it and the warp a strong stretched rubber thong, just as a runner bean in the garden winds itself on to and up its supporting stick.

Using such a cheap and easy method of attachment, one can affix all manner of instruments to all sizes of wire, cable, or rope and secure a firm non-slip grip without trouble.

The rather heavy inclinometer is pictured fastened securely on to a very smooth brass wire no thicker than ordinary water-bottle wire. To facilitate attachment by one person working alone, the side of the bracket which is bound on to the warp has since been fitted with prongs after the manner of the wooden rods fixed across the tops of some of the bottles pictured. This makes it very easy to effect attachment by winding a lot of stretched office rubber bands round and round bracket-rod and warp in an obvious manner.

It does not matter if the warp twists at all because the rectangular inclinometer as pictured can swing all round it and still maintain parallelism—just as the passenger cages of the " Big Wheel " at a fair move round its axle.

There is a filling point (unscrew the domed knob) and also an air vent controlled by a removable grub screw. Inwards thumb and finger pressure exerted on the two small spring-loaded levers either side of the filler knob releases the rectangular box from its bracket.

The idea is to have a battery of such inclinometers standing in a bath of hot water on deck with their brackets alongside as the cable is veered. With such a situation the brackets are simply affixed and the boxes no less easily clipped in. This inclinometer has worked well in tests and has congealed conveniently in about 20 minutes, but it would be improved by being made semi-circular to avoid preferential congelation in the corners, and should be lighter.

If used on the warps of a trawl being towed, there will be some lateral pressure on the box on account of the warps not leading dead astern. The rectangular inclinometer might not remain completely pendulous under such circumstances unless unduly weighted along its bottom edge. The result might be that the pendulum would not then give the true reading for slope which it provides when towed dead astern. If round jelly bottles be used as slope indicators however, there can be no difficulties due to any rolling out of a pendulous position. If the need be to use them on a thin stranded wire of water-bottle type, they can be used in clamp-fitted holders, as was kindly done for the writer aboard the German research vessel *Gauss* by Dr. JOSEPH in March 1955, during a cruise in the North Sea. Two results obtained by Dr. JOSEPH are pictured (Fig. 3). The slope of the firm slant interfaces which can be very clearly seen was measured with ease by means of a simple goniometer made specially for the purpose.

Dr. JOSEPH towed a terminally-weighted wire astern with six of the clamp-fitted jelly bottles affixed at equal intervals along its underwater part. The clear results he got revealed overall downwards concavity of the curved wire with increase of slope towards the weight.

On another occasion he streamed a buoy astern on a considerable length of wire with a weight hung on about half way along it. Jelly bottles spaced equally, four on each side of the weight, revealed very clearly the opposite slopes of the two halves of the wire. Between the ship and the weight the wire took on a downslope very little removed from straight, though with a very slight downwards concavity. From the weight to the buoy the wire sloped fairly steeply upwards with a very pronounced upward concavity.

The results will be reported upon in detail on some later occasion when more have been added.

The two bottles pictured (Fig. 3) had been used on opposite sides of the weight, which was hung midway along Dr. JOSEPH's towed buoy-line. With his jelly bottles the writer has preferred not to use clamps for attachment purposes, but to employ the same sort of method as was described above in connection with the rectangular inclinometer. To do so avoids limitation of use to one sort and size of line.

An accompanying picture (Fig. 4) shows two jelly bottles after use in experiments recently conducted in the Crouch estuary from a research vessel belonging to the Ministry of Agriculture and Fisheries. Mr. D. WAUGH of the Burnham Fisheries Laboratory very kindly afforded the facilities and gave yeoman assistance. In this picture the convenient goniometer made by Dr. JOSEPH for measuring the jelly slopes is also to be seen.

The jelly bottles illustrated are of the usual heat-resistant glass and are of the compass-containing type. To affix them easily to lines of any size or nature the following was done:

A convenient length of clean, strong and heavily-lacquered wooden dowel rod was

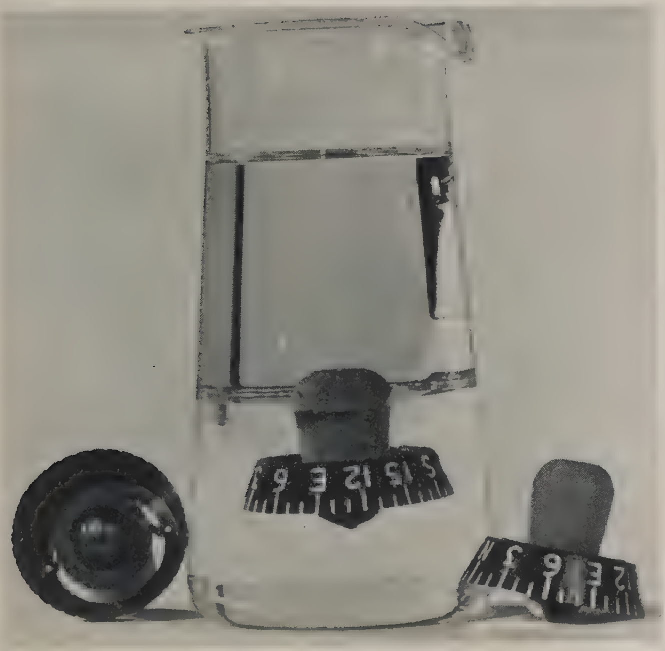

Fig. 1. For explanation see text.

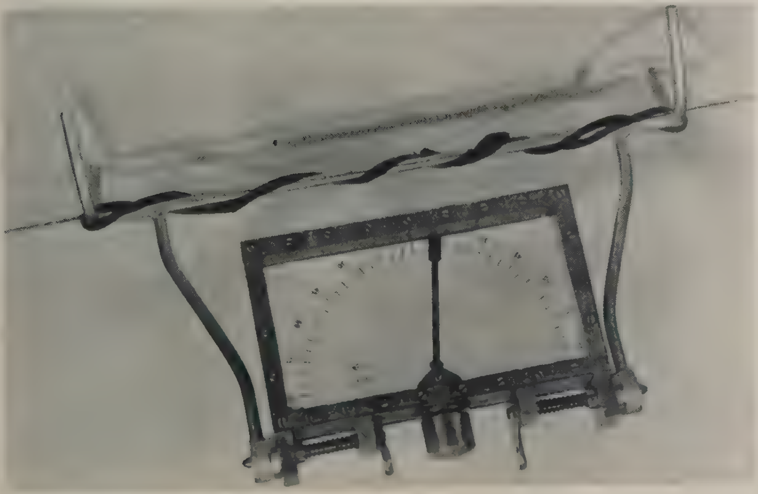

Fig. 2A. For explanation see text.

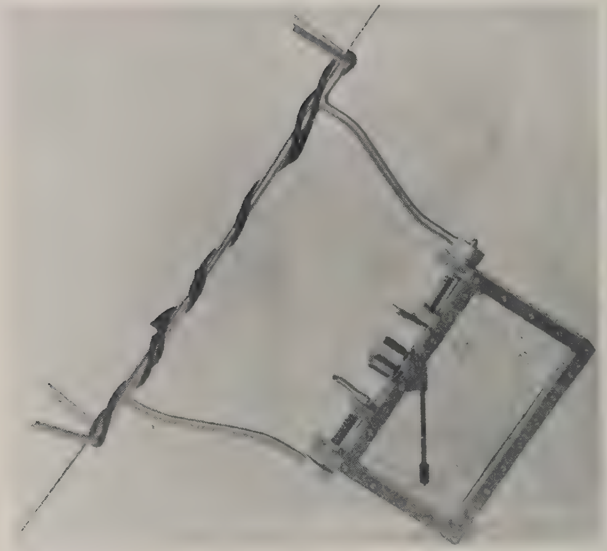

Fig. 2B. For explanation see text.

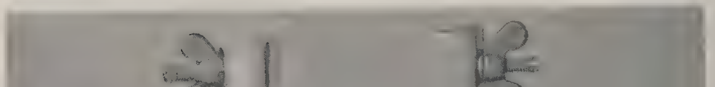

Fig. 3. For explanation see text.

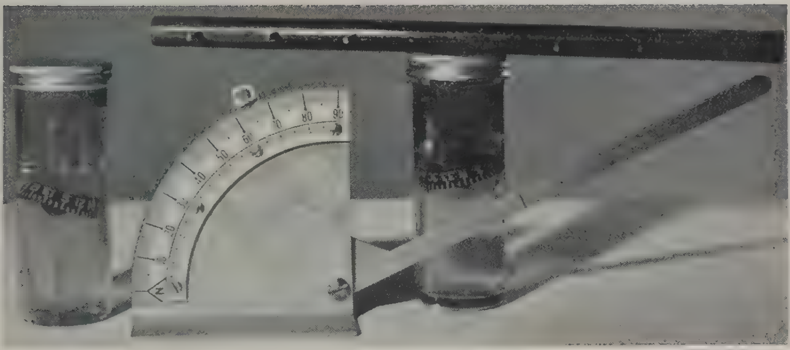

Fig. 4. For explanation see text.

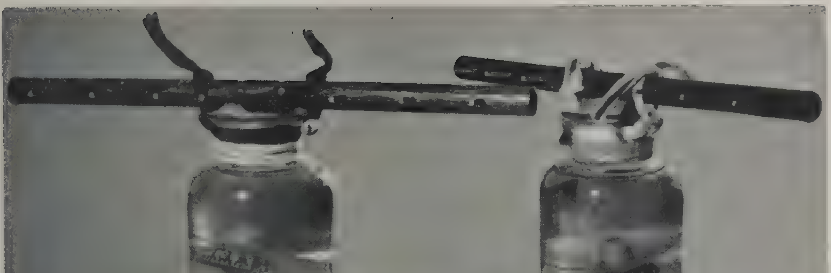

Fig. 5. For explanation see text.

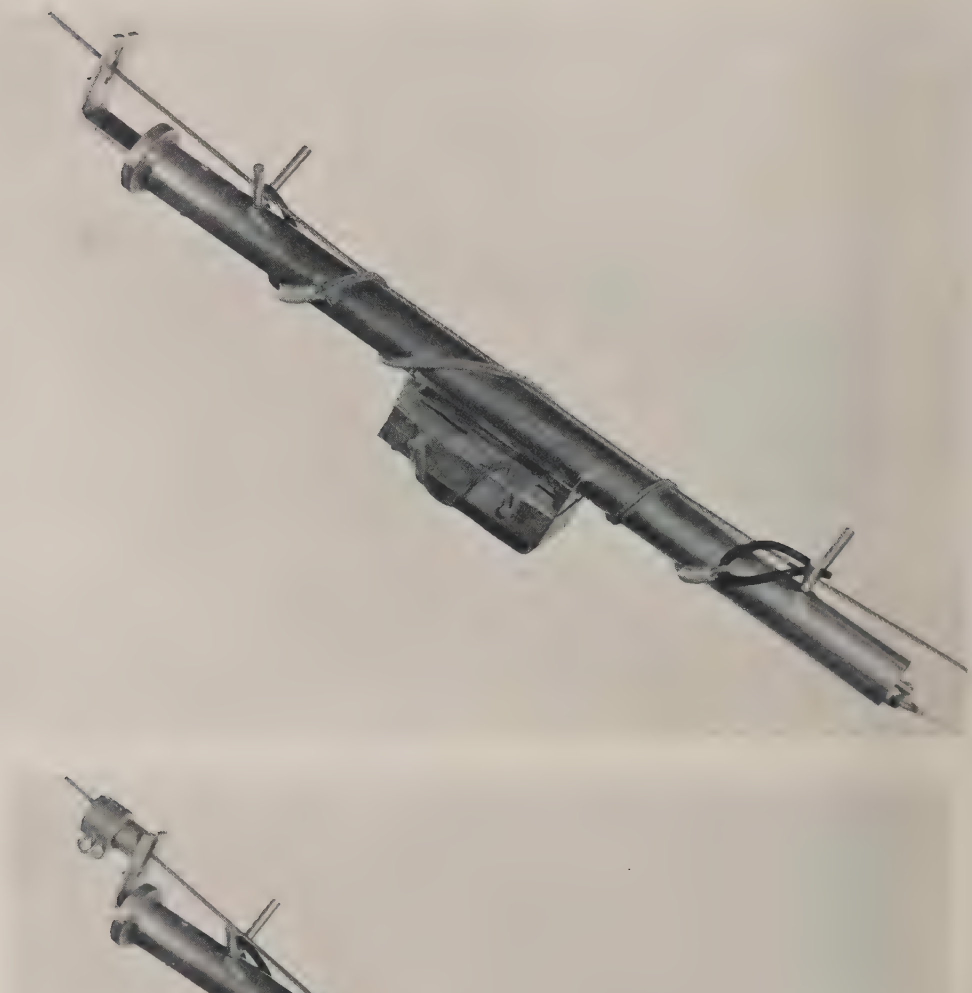

Fig. 6A and B. For explanation see text.

fastened immovably and diametrically across the top of the aluminium screw-on closure cap. This was effected by riveting on from the underside. In the cap is a disc of kerosene-resistant artificial rubber. On both sides of the disc the round wooden rod has had thin but stiff metal bars driven through it to present prongs projecting equally either side. Such a rod can be seen illustrated in another of the pictures (Fig. 5).

With this convenient arrangement all that is necessary to effect secure attachment is to hold the bottle-carrying rod against the rope, wire or cable with one hand, and to hook good quality office rubber bands on to the individual prongs in succession—stretching them, winding them whilst in tension round rod and cable, and hooking their other ends on to whatever prong offers to hold them tight.

The last-mentioned picture (Fig. 5) shows a pair of compass-containing jelly bottles which had also been used in the Burnham experiments. In this case the bottles are wide-necked pyrex bottles which are a standard list item of laboratory furnishers. With them, the attachment rods were secured on to the cork closure bungs by means of slender washer-loaded bolts and small nuts.

Various additional (and much more elegant) mountings for the compass-containing jelly bottles were made by Mr. A. J. Woods of Messrs Kelvin & Hughes. He has been associated with the writer throughout the experiments, and is making improved devices (to be spoken of below) in the course of continuing collaboration.

The excellent little aircraft ring compasses used in the experiments were made and kindly loaned by Messrs. Kelvin & Hughes. For reasons of cost and space Mr. Wood's additional mountings are not illustrated in this article, but it should be mentioned that the two extra kinds which he constructed both made use of a pronged attachment bar and rubber bind-on bands. One of them simulated the " Fair Wheel " characteristics of the bracket-mounted rectangular inclinometer earlier described (Fig. 2A and 2B).

APPLICATION TO PELAGIC TRAWL INVESTIGATIONS

Because there is a likelihood that commercial fishermen of future years will find an ever-increasing need to operate on the stocks of non-bottom fish living in deep-water oceanic areas, it is probable that the passage of time will invest pelagic trawling with more and more importance.

From inquiries made of fisheries research experts who concern themselves with the modern one-ship pelagic trawl, need exists to know much more than is known at present about it.

In the course of the experiments carried out in the Crouch estuary with jelly bottles, a situation resembling " fishing in reverse " with such a net was staged. Under Mr. Waugh's direction two boats were anchored a measured distance " X " apart across the stream, and a line some " 2X " (and other multiples of " X ") long was streamed from them—with one end secured at each boat and a large plankton net plus other drogue objects attached to the mid-point of the line.

In such circumstances, with a series of compass-containing jelly bottles secured on to each half of the streamed line, it should be easily possible to determine the mean angular divergence. By multiplying the total length of the line into the sine of half that angle, one should get a value equal to the distance of separation of the two anchored boats.

There were a few difficulties during the tests as can readily be imagined. For instance, a strong pull by the drogues must urge the boats to close somewhat on each other, whilst less than a really strong pull must leave the lines bowed to some extent. Nevertheless, the results were amply good enough to invest the application of the idea to studies of the pelagic trawl with real promise.

Certain full-scale experiments are envisaged thanks to expressions of interest and the promise of facilities from the two British fisheries laboratories. Of an ample assemblage of the compass-containing jelly bottles, half would have their " upperworks " enamelled red for attachment on the port warp, whilst the other half would have green floats and would go on the starboard warp.

In a first investigation the average overall downslope of both warps will be worked out from the mean of the jelly slopes, and the fishing depth of the net estimated accordingly. From the compass readings of the bottles the course of the warps as projected on the sea-floor will be derived and an estimate of the horizontal gape of the net made.

Apparently Dr. SCHÄRFE holds the view that useful conclusions as to horizontal net gape can even be made from noting only the separation angle of the warps behind the slip hook. This he does by means of his special device the " Spreizmesser ".

Since the investigating ship will have an echo-sounder the net tests could be done in a chosen area with a flat bottom so that it could always be known that the foot-rope would never be higher off bottom than a distance " H ". If, when the net was shot, a length of thin Kelvin wire of length about 1½H or 2H carrying an object like a smooth cannon-ball at its free end were hung from the bottom of the net, then, if several jelly bottles went down on this wire, one would learn on hauling what its slope had been and so would know how high above bottom the foot-rope had ridden during the tow. One would then have data enough to make an estimate of the vertical gape of the net. In a subsequent investigation much better things will be attempted:

A drogue of nearly neutral buoyancy will be towed inside the net from the midpoint of a light line of not much greater length than the distance the net doors would be apart if the net were stretched out tight on the quayside. An array of compass-containing jelly bottles on each half of such a line will give a much better triangulating situation with sound promise of an acceptable determination of horizontal gape.

How the same sort of thing could be done to investigate vertical gape at different points will readily suggest itself.

For some of the determinations the jelly bottles would not need to contain compasses.

The need to weigh a few considerations has led to postponement for the time being of the full scale net tests from a fisheries research vessel. For one thing there is the need to hit upon a long-enough timing (congelation period) as already stated. Then, although one could not possibly devise any other slope and direction indicators as simple as the jelly bottles, it is a fact that difficulty attaches to reading the compass directions precisely enough when (as so often must happen) the compasses are not on an even keel but are awkwardly canted.

Where slope only is needed, recourse will be had to a gelatine-filled perspex cylinder containing a rolling clinometer furnished with a finger which travels over a protractor. With this device (now being made), there will be no need for two liquids and no need to measure jelly slopes with an external goniometer.

At the time of writing this there is also being made (by my collaborator, Mr. A. J.

WOODS of Messrs Kelvin & Hughes) an instrument which is in effect a rolling clinometer containing a compass which will always remain on an even keel. This also will be contained in a perspex cylinder filled with gelatine only, and it too will have a contained protractor permitting slopes to be read to one degree or so. Its compass will be pivoted and not dependent upon buoyancy of a small float. This is an advantage because no depth limit will apply as it might if risk existed of a float being compressed by water pressure to a state of nil buoyancy. When these devices have been fully tested and made in sufficient number, the full scale net tests will be embarked upon without delay and with confidence. Sight will not be lost of the need to ensure that the compasses are held a sufficient distance from the warps to escape any disturbing influence of the latter.

So far we have discussed mainly the measurement of slopes of modest magnitudes below the horizontal. We turn now to slopes measured as departures from the vertical.

OFF-VERTICAL SLOPES: THE UNDERWATER COURSE OF DEEP-SEA WIRES AND CABLES

Our first concern was to establish a means of checking the showings of the wire-angle gauge to which earlier reference has been made above (CARRUTHERS, 1954 B). The need is to discover whether the pendulum gives a true value for the slope of a hydrographical wire (with its load of water bottles) when the observing ship is somewhat lively. It was decided to use jelly bottles to make an adequate series of tests.

The first requisite was to devise a way of using them on the hydrowire without interfering with the operation of water bottles and the wire-angle gauges at the same time. The way chosen was to construct a simple " messenger-passer " easily attachable to the wire and able to carry a compass-containing jelly bottle held firmly parallel to the latter. It would then only be necessary to fit the fall-away messenger hung beneath such a device with an extra-long lanyard, to enable the two German clamp-on jelly bottles (Fig. 3) to be used as well as the compass-containing jelly bottle. This latter would be housed in a sort of little sentry box attached to the " messenger-passer ". Such an arrangement would furnish three jelly slope values and one direction reading for comparison with the readings of the wire-angle gauges under test.

Illustrations of the simple instrument made by Mr. WOODS to the writer's design are presented (Fig. 6A and 6B). The first (6A) shows the situation before the arrival of a messenger from above, i.e. with the fall-away messenger still hanging beneath. The second (6B) shows the situation after the strike of the messenger from above, i.e. with the fall-away messenger gone down to trip other instruments below.

The device consists of a brass tube attachable by stretched rubber thongs to the hydrowire. Running down its interior is a flat bar of brass with a small hinged piece at its lower end. So long as this is bent upwards and contained in the tube, a messenger can be hung from it, but as soon as the central bar is pushed down to full extent the messenger must fall away. The central bar is bent over at the top as shown, and is forked to receive the wire. A length of it near the top of the tube is slotted, and through this slot a short length of thin glass rod can be passed and seated in a cupped collar at the top of the tube. The glass rod takes the weight of the internal bar and the hanging messenger when the device is cocked. The impact of a messenger from above infallibly breaks the glass rod and lets the pendant messenger fall away.

The compass-containing jelly bottle is housed in the little fastened-on brass box discernible on the face of the tube. A fin fused on one side of the bottle seats in a slot cut into the tube to provide direction fixation, and the bottle is held firmly in place by means of rubber bands as illustrated.

Six fathoms of water in the River Crouch afforded enough messenger travel for two wire gauges to operate with the " messenger-passer " in between them. The latter always functioned without fail. At the time of writing this the deep-sea tests to check the showings (pendulum behaviour) of the wire-angle gauges in the manner described, are in progress aboard the Royal Research Ship *Discovery II*.

If it were desired to observe the slope magnitudes and directions of a thick trawling cable leading all the way down to a trawl or dredge being dragged over the deep ocean floor, it would not be possible to use jelly bottles for time reasons. Also, any messengers for the use of which a devised method might call would necessarily have to be of rather mammoth size—each one something like a yard of heavy iron tube split and hinged to go on the cable. It is suggested that a simple " messenger-passer " after the style of that described could be made " rough, long, and strong " with a thin tight metal rod of water bottle wire diameter held a small distance off from it (but parallel to it), strained between two short spurs projecting out at right angles respectively at top and bottom. If such crude devices were fastened on to the cable at desired intervals in the manner already described, a wire-angle gauge could be operated at the bottom of the thin offset rod in each case. This could be done quite simply if, when a giant messenger struck to break the short length of thick glass rod or small phial which would be necessary in such case, a daughter messenger of ordinary weight and size were released to run down the offset rod to trip the gauge quite harmlessly.

OTHER POSSIBILITIES

In spite of the wide variety of current-meters already in existence, there remains a real need for one which could be used to make all-weather absolute observations of near-bottom currents from anchored vessels. The numerous and very convenient lightships are in mind. The problem has always been how to get acceptable records from a lively ship, and the suitable use of jelly bottles suggests itself as offering escape from the difficulties imposed by ship movement, because they would be self-damping systems.

If a length of Kelvin wire carrying a heavy terminal plummet were let down from a lightship, it would be easy to stream tow-nets from it at any desired depths. The nets could be made of very wide mesh fishing net near their mouths, and the rest of stramin. If streamed on up-and-down bridles the rings would not rotate. In such case there could be a horizontal diametric brass rod across each net mouth, and on it could be hung a semi-circular swinging plate carrying a compass-containing jelly bottle suitably mounted on its reverse.

Using some such simple arrangement with limp connection to the suspension line, absolute measurements of currents could, it is held, be acceptably made during quite bad weather. Such a method is well worth trying because of the great opportunities which exist for working from anchored vessels. The necessary calibrations would, of course, have to be made against logship runs. When the compass-containing and depth-ignoring rolling clinometer spoken of above becomes available with slope-reading possible to one degree and compass always on an even keel, the possibilities will be greatly enhanced. Then, the simple current-measuring instrument envisaged should be able to give good service used from a moving ship, to reveal currents differences between small and great depths.

It remains only to remark that such simple congealing inclinometers with direction-indicating powers as are being made, could be very usefully employed in non-captive instruments sent down to the ocean depths to record the bottom water movements there. The working principle would be that of the bathygraph of EWING and VINE, which achieves self-ascent under the lift of an oil-filled balloon after the detachment of ballast left on the ocean floor. This is of course the principle of Professor PICARD's bathyscaphe but, as EWING and VINE remark, " the problem of locating the apparatus after it has reached the surface is a serious one ".

ACKNOWLEDGEMENTS AND NOTE

Thanks are expressed to Mr. A. J. WOODS for his very valuable collaboration and instrumental ingenuity; to Mr. D. WAUGH for generous help when carrying out tests; and to Doctors BÖHNECKE and JOSEPH for trials made aboard the German research vessel *Gauss*.

Though this is perhaps a strange finish to a paper such as the foregoing, the writer is obliged to remark that the jelly bottles come specifically under the coverage of a patent which runs in most countries having important fisheries. The patent in question relates to the Current Cone for which the licence holders are Messrs Kelvin & Hughes. From them the final models of the slope-and-direction indicators will presumably be procurable in due course.

REFERENCES

CARRUTHERS, J. N. (1954 A), Some inter-relationships of oceanography and fisheries. *Arch. f. Met., Geophys. u. Bioklim.*, B, **6** (1/2), 167–189.
CARRUTHERS, J. N. (1954 B), On the instrumental measurement of line-shape under water. *Deutsche Hydrogr. Zeits.*, **7** (1/2), 1–14.
SCHÄRFE, J. (1953), Geräte zur Messung an Schleppnetzen. *Die Fischwirtschaft, Bremerhavn*, (1/2).

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The fauna of an inter-tidal mud flat

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Summary—1. An account is given of the fauna of an inter-tidal mud flat (North Bay) in Kyle Scotnish, Loch Sween, Argyllshire.

2. The distribution of the more important species of the fauna over the shore is discussed.

3. Some indications are given of the growth rates of four lamellibranchs, *Macoma*, *Scrobicularia*, *Cardium* and *Mytilus*.

4. The changes in the density of the fauna are followed from 1943 to 1946, and the possible beneficial effects of the fertilization of Kyle Scotnish on the bottom fauna of the inter-tidal zone are reviewed.

INTRODUCTION

SOME ACCOUNT has already been given of the bottom fauna of Kyle Scotnish—a northern arm of Loch Sween, Argyllshire (RAYMONT, 1950), but that investigation was confined to the fauna below low water mark. Very little inter-tidal shore exists in Kyle Scotnish, but near the head of the loch there is a fairly extensive mud flat which is designated in the text North Bay (Fig. 1). Although a small stream enters the area, most of the flat is not estuarine. It was thought desirable to investigate the fauna of the mud flat, since most of the work done on muds in Great Britain concerns estuaries (e.g. FRASER, 1932; REES, 1940; BEANLAND, 1940; SPOONER and MOORE, 1940). Since also the main work in Kyle Scotnish has been concerned with the effect on general productivity of the addition of nitrate and phosphate fertilizers, it was decided to attempt to correlate population changes in the mud flat with the effects of fertilization.

The investigation extended over three years commencing in November 1943. Sampling over such a short period cannot give results on which very definite conclusions may be based. Nevertheless, as the work at Loch Sween had to be ended in 1946, the samples have been worked through and some account of the work is presented.

METHODS

Sampling was confined to an autumn (November) and summer (July) period each year. Four transects were planned across North Bay, sited on permanent marks on shore, and three or four stations were selected at approximately equal distances along each of the four lines, beginning near High Water and extending to Low Water (Fig. 1). Altogether fourteen stations were regularly sampled. No exact tidal levels were taken, as the tidal range right at the head of Loch Sween is small, and moreover the tides are irregular, the periods of exposure of the flat being very largely dependent on the prevailing wind.

Various sampling techniques were tried during November 1943 involving the digging of a square (side 0·5 metres) and sieving the material, but such a procedure proved too laborious. In the method finally adopted a quadrat (side 0·5 metres) was dug to a depth of 10–12 cm, the material passed through a coarse (9·5 mm) sieve, and only the larger bivalves exceeding 10 mm length retained in the sieve were counted. At the same station three small " auger " samples were also taken. The auger consisted of a metal cylinder 10 cm diameter, 23 cm height, with a handle at the top. The auger was pushed into the substratum to a depth of 10 cm and then pulled out again with its mud core. Usually the consistency of the mud was such that very little of the core was lost. Each of the auger samples was passed separately through a 1 mm sieve and all the organisms retained were preserved in alcohol and sorted later.

In estimating the total population at any station, the three auger samples were analysed first. Any bivalves exceeding 10 mm length in these samples were discounted, and the numbers of all other organisms then averaged. To this population was added the number of large bivalves *only* (>10 mm) obtained from the ¼m² quadrat sample at the same station. The whole population was expressed in numbers per m².

The shore of North Bay is covered by a soft mud with a little sand, and with shell and gravel some few inches below the surface. There are a few isolated boulders and some patches of weed (mostly *Fucus vesiculosus*). None of the fourteen sampling stations was sited in weed or near boulders. Even so, the three auger samples at any one station could show considerable differences. Some idea of the great variation which could occur is given for two stations in July 1946, when six auger samples (A–F) were taken at a few feet distance radiating from the sampling point, instead of the normal three samples taken close together (Table I). The last columns in Table I, showing the average population based on the usual three augers and also an average based on six samples, indicate that the normal three samples probably give a reasonable picture of the average density of a sampling station. In many of the regular series of samples the agreement between the three auger samples was remarkably good.

Table I

Variation in auger samples at two stations: Tr. 4, *St.* 2 *and Tr.* 3, *St.* 4, *July* 1946. *A–F represent actual numbers in* 6 *samples taken a few feet from each sampling point. The average of* 3 *samples* (*A*, *B and C*) *has been used for calculating the population per m²*

	Transect 4 Station 2								*Transect 3 Station 4*							
	Samples						*Average A, B, C*	*Average A–F*	*Samples*						*Average A, B, C*	*Average A–F*
	A	*B*	*C*	*D*	*E*	*F*			*A*	*B*	*C*	*D*	*E*	*F*		
Cardium	—	—	2	—	2	—	1	1	5	3	—	—	—	4	3	2
Macoma	—	—	1	—	1	2	+	1	—	2	1	2	—	2	1	1
Hydrobia	35	54	46	26	39	56	45	42	53	20	17	53	17	86	30	41
Littorina	—	—	—	—	1	—	—	+	—	—	—	—	—	—	—	—
Oligochaetes	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	1
Crustacea	2	1	6	2	1	10	3	4	5	1	—	—	—	—	2	1
Chironomids	—	1	—	—	1	—	+	+	1	—	—	—	—	3	+	1
Nephthys	1	—	—	1	—	2	+	1	1	—	1	1	1	—	1	2
Pygospio	2	5	1	2	1	5	3	3	1	—	—	1	—	—	+	+
Phyllodocids	1	—	—	—	—	—	+	+	—	1	—	—	—	—	+	+
Total	41	61	56	31	46	75	53	52	66	27	19	61	18	95	37	48

The efficiency of the sampling by means of a single ¼m² quadrat for the larger bivalves was tested by taking two quadrats at each station instead of the usual one. There was normally reasonable agreement between the pairs of samples (Table II). Occasionally there were large discrepancies (e.g. Tr. 1, St. 3 and Tr. 3, St. 3), which appear to have been due mainly to a dense but patchy settlement of *Mytilus*. The bivalve population for July 1946 has been calculated by averaging the two quadrats taken.

The loss during transport of an auger sample has occasionally made it necessary to calculate the average population at a station on the remaining auger samples. On certain occasions also, at the lowest station of a transect, it was necessary to sample the mud fauna with a small grab, as the area remained covered with water for several days owing to the irregular tides. Generally the whole sampling for the fourteen stations took some three to four weeks.

Table II

Variation in quadrat samples. Two $\frac{1}{4}m^2$ quadrats, A and B, were taken at each sampling station. Numbers indicate the counts of large bivalves (>10 mm) taken in each $\frac{1}{4}m^2$ sample.

Station	*Macoma*		*Scrobicularia*		*Cardium*		*Mytilus*		*Total*		*Total Average*
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	
Transect 1:											
1	0	0	36	30	0	0	1	1	37	31	34
2	0	1	3	0	24	3	7	7	34	11	22·5
3	0	0	0	0	10	23	138	56	148	79	113·5
Transect 2:											
1	2	0	4	2	0	0	0	0	6	2	4
2	0	2	35	26	0	0	5	1	40	29	34·5
3	4	0	0	2	0	1	55	55	59	58	58·5
4	0	0	0	0	1	0	3	10	4	10	7
Transect 3:											
1	0	1	5	5	0	1	0	1	5	8	6·5
2	0	0	12	17	1	1	0	0	13	18	15·5
3	0	0	10	11	5	3	16	4	31	18	24·5
4	0	1	1	1	28	12	69	57	98	71	84·5
Transect 4:											
1	0	0	2	12	14	0	0	3*	16	15	15·5
2	0	0	0	0	1	1	0	0	1	1	1
3	0	0	0	0	4	4	0	40	4	44	24

* = 1 Mya *included*

Table III

List of fauna taken in regular samplings in North Bay

Polycladida
Nemertini
Peloscolex benedeni Udekem
Platynereis dumerilii (Audouin & Edwards)
Nereis diversicolor O. F. Müller
Kefersteinia cirrata (Keferstein)
Phyllodoce maculata (L.)
Eteone longa (Fabricius)
Notophyllum sp.
Glycera sp.
Nephthys hombergi Lamarck
Nephthys sp.
Scoloplos armiger (O. F. Müller)
Pygospio elegans Claparède
Pectinaria koreni Malmgren
Arenicola marina L.
Capitella capitata (Fabricius)
Heteromastus filiformis (Claparède)
Fabricia sabella Ehrenberg
Maldanidae
Syllidae
Macoma balthica (L.)
Scrobicularia plana (da Costa)
Cardium edule L.
Mytilus edulis L.
Mya arenaria L.
Modiolus sp.
Kellia suborbicularis (Montagu)
Abra prismatica (Montagu)
Paphia decussata (L.)
Paphia pullastra (Montagu)
Hydrobia ulvae (Pennant)
Littorina littorea (L.)
Littorina littoralis (L.)
Cylichna cylindracea (Pennant)
Philine aperta (L.)
Acera bullata O. F. Müller
Amphipoda
Gammarus sp.
Corophium volutator (Pallas)
Isopoda
Jaera sp.
Idothea granulosa Sars
Sphaeroma rugicauda Leach
Crangon vulgaris L.
Praunus neglecta G. O. Sars
Chironomus salinarius Kieff.
Chironomid larvae
Chironomid pupae
Other larval Diptera
Ophiura texturata Lamarck

In many cases, particularly among soft-bodied animals, the methods of sampling and sieving broke up the material so that identification has not been taken further than the genus. Some animals (chironomid larvae) have not been identified further than family, although the dominant species has been noted. The list of fauna has been constructed mainly from the identification of favourable specimens preserved in good condition.

GENERAL COMPOSITION OF THE FAUNA

Although no account was taken of the small bottom animals (protozoans, nematodes, very small crustaceans, etc.) which were not usually retained by the sieve, more than 40 species were recorded from the area. Of these (Table III) comparatively few appeared to be regular members of the fauna. Four bivalves (*Scrobicularia*, *Macoma*, *Cardium*, *Mytilus*), two gastropods (*Littorina* and *Hydrobia*) and several polychaetes (*Arenicola*, *Nereis*, *Nephthys*, *Heteromastus*, *Pygospio*, *Phyllodoce* and *Eteone*), with two other groups of animals (oligochaetes and chironomid larvae) were the most important numerically. Crustacea were very poorly represented throughout: the average population rarely reached even 1% (Table IV). Echinoderms were practically absent altogether; only an occasional small *Ophiura texturata* was taken.

Table IV

Average population for whole North Bay area based on 14 *regular stations.*
(All numbers per m^2*)*

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Bivalves (large)	110	66	44	44	130	125
Bivalves (small)	149	418	233	206	1,064	129
Hydrobia	10,077	7,640	10,143	6,977	13,759	6,961
Chironomids	686	318	454	548	1,526	365
Oligochaetes	2,394	984	948	712	1,288	415
Crustacea	121	29	60	66	56	101
Polychaetes	594	778	936	1,199	470	285
Other organisms	91	91	249	157	415	313
Totals	14,222	10,324	13,067	9,910	18,708	8,694

The gastropod *Hydrobia ulvae* was overwhelmingly dominant in number. The average population calculated for the fourteen stations in North Bay showed that at times *Hydrobia* formed 80% of the total population, and that it never fell below 70% during the whole period of the investigation. *Hydrobia*, with oligochaetes (chiefly *Peloscolex benedeni*), and chironomid larvae (mostly *Chironomus salinarius*)* together dominated the fauna over the whole area, comprising approximately 90% of the whole population (Table V).

There was a slightly lowered percentage for these three organisms in July 1945, which was due to an increase in one species only—*Pygospio*. This polychaete formed 48% of the polychaete population in July 1945 (Fig. 4) and it occurred in 13 of the sampling stations.

In November 1945 young bivalves made an appreciable contribution to the total fauna (Table IV), but only two species were abundant—*Cardium* and to a lesser extent

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* I am indebted to Professor A. THIENEMANN for this identification.

Mytilus. In the summers of 1945 and 1946 young mussels settled in enormous numbers over North Bay, but they usually did not survive for very long probably because of the soft substratum. The ordinary samplings did not reflect the full extent of these temporary settlements, but special collections made in the summer of 1945 after the spatfall in Kyle Scotnish and in two nearby other unfertilized arms of Loch Sween (Linne Mhurich and Sailean More) demonstrated the richness of the settlement in parts of North Bay (Table VI). Larger *Mytilus* were not abundant in North Bay; in fact more were present in Sailean More (Table VI).

Table V

The percentage of Hydrobia, *oligochaetes and chironomid larvae based on the average populations for North Bay*

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
$\% \frac{\text{Hydrobia}}{\text{Total fauna}}$	71	74	78	70	74	80
$\% \frac{\text{Hydrobia} + \text{oligochaetes} + \text{chironomids}}{\text{Total fauna}}$	93	87	88	83	89	89

Table VI

Abundance of large and small mussels in three arms of Loch Sween, Summer, 1945. *Kyle Scotnish is the only fertilized water.* (*All figures are numbers per m*^{2})

		< 10 *mm*	10–40 *mm*	>40 *mm*
KYLE SCOTNISH—North Bay (Fertilized)	Area 1	9,300	4,300	ca. 10
	Area 2	396,000	556	136
LINNE MHURICH (Unfertilized)	Area 1	0	160	184
	Area 2	32	8	72
SAILEAN MORE (Unfertilized)		9,712	2,088	1,068

Of the " other organisms " in North Bay (Table IV), the commonest were *Littorina littorea* (almost all juvenile), *Cylichna*, nemertines and occasionally *Philine.* The slight rise in " other organisms " late in 1945 and 1946 was accounted for almost entirely by young *Littorina. Acera bullata* occurred in fair numbers in the deeper waters of Kyle Scotnish during 1946, and it appeared in the shore samplings during July of that year.

ZONATION

Although the stations were not definitely related to exact tide level, for each transect Station 1 was sited high up on the flat, and the last station (Station 3 or 4) close to low water. Some attempt has therefore been made to relate very broadly the distribution of the more important members of the fauna to level on the shore.

Of the bivalves, *Macoma* was fairly evenly distributed across the shore, while *Scrobicularia* was somewhat more abundant at upper and middle levels (Fig. 2). *Mytilus* was absent near high- and mid-tide levels, and increased towards low water. In Transect 4, however, it was abundant in the middle region as well as towards low water, but still avoided the upper levels (Fig. 2). This difference may possibly be explained by the fact that Transect 4 was taken on a different portion of the shore close to a small permanent stream which ran across the mud (Fig. 1). This difference in distribution was also seen for *Cardium*: while in Transects 1–3 this bivalve was practically absent near high water mark and was common from mid-tide levels and towards low water, in Transect 4 *Cardium* was commonest at the uppermost levels and decreased in abundance down the shore (Fig. 2).

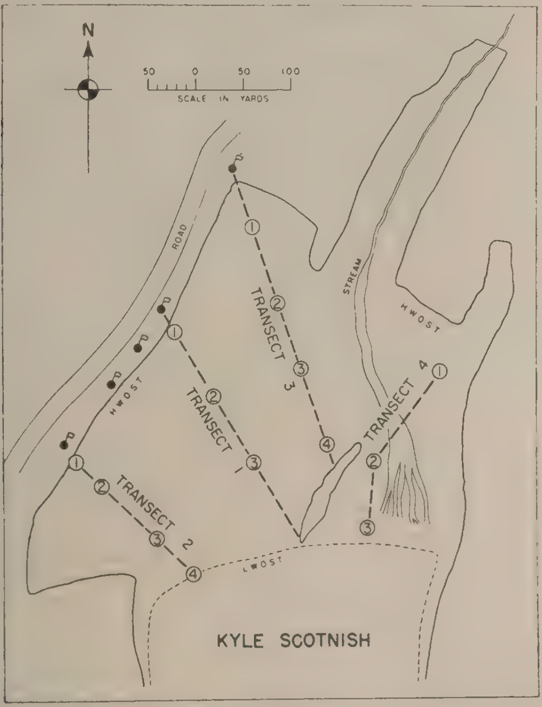

Fig. 1. Sketch map of North Bay mud flat at head of Kyle Scotnish, showing positions of the four Transects. Numbers along Transects indicate Stations. Flagged dots = permanent poles on road-side used for bearings

Some of the polychaetes also showed fairly obvious distributions. *Nereis diversicolor* was hardly represented below mid-levels on the shore and was at its maximum at the uppermost stations (Fig. 2). This distribution applied to Transects 2 and 3; along the other Transects *Nereis* occurred hardly anywhere throughout the sampling period. *Nephthys* contrasted sharply with *Nereis* in that it was practically absent from the upper levels and increased sharply towards low water (Fig. 2). *Nephthys* also occurred quite commonly below low water mark. There is again the suggestion

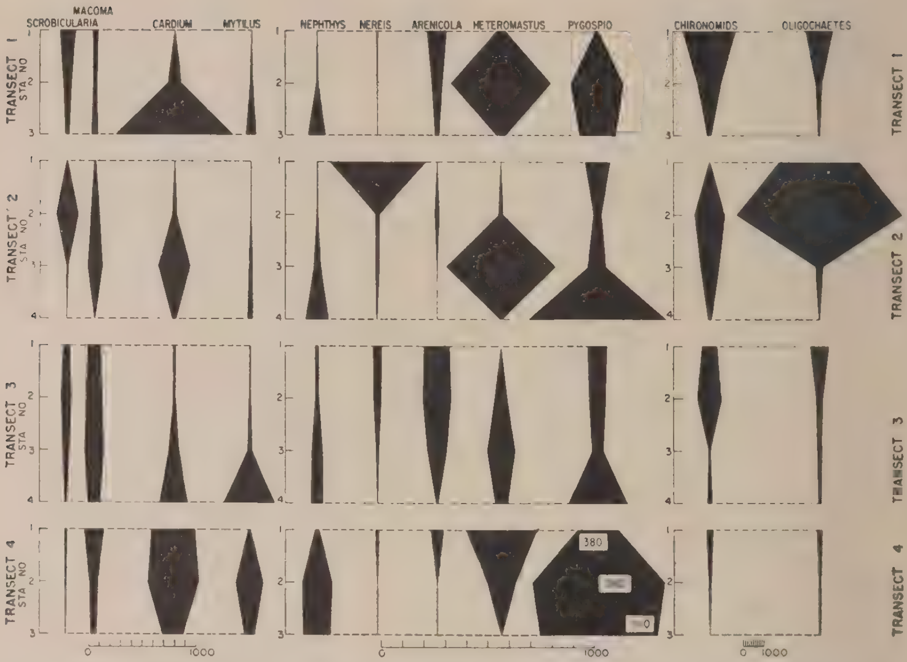

Fig. 2. The distribution of the more important lamellibranchs and polychaetes; also of chironomid larvae and oligochaetes. Along each transect, the stations are taken as equidistant down the shore, St. 1 being near high water mark. The numbers are densities per m² calculated as averages of the populations of 6 sampling dates. Note: A different scale has been used for *Pygospio* in Transect 4

that Transect 4 was generally on a somewhat lower level of the shore. *Nephthys*, for example, was commonest at the mid-station of this Transect instead of at the lower station. *Heteromastus* also appeared to be reaching its maximum density at the high level of the shore in Transect 4, whereas in Transects 1–3 *Heteromastus* was absent

Table VII

The distribution of Hydrobia ulvae *over North Bay. The population of each station is expressed per m² and represents the average of the 6 sampling dates. Numbers in brackets are rounded figures based on averaging 3 July samples*

	Transect 1	*Transect 2*	*Transect 3*	*Transect 4*
Station 1	8,529 (8,300)	6,021 (6,700)	10,593 (9,200)	16,246 (15,300)
Station 2	7,974 (6,700)	9,809 (10,600)	14,366 (10,500)	9,264 (4,600)
Station 3	5,944 (3,100)	9,759 (5,600)	16,149 (12,600)	1,903 (300)
Station 4		283 (300)	12,793 (6,900)	

from the uppermost station, was sparsely distributed towards low tide, and was quite sharply limited to the middle regions of the mud flat (Fig. 2). *Arenicola* appeared to decrease towards low tide levels, especially in Transect 4, while the very abundant *Pygospio*, while occurring across the whole shore, was more abundant at mid- and low-tide levels (Fig. 2).

Both chironomid larvae and oligochaetes (*Peloscolex*) were commonest over the mid- and upper parts of the shore, and decreased sharply towards low-tide mark (Fig. 2). Perhaps they avoided the higher salinities towards low water, although in Loch Craiglin chironomids occurred over the bottom where the salinity was about 30‰ over most of the year (RAYMONT, 1947). The distribution of juvenile *Littorina* was rather irregular, although on the whole they were less abundant towards low water.

The commonest gastropod (*Hydrobia ulvae*) showed no very clear zonation, being widely distributed with populations of several thousand individuals per square metre over most of the shore (Table VII). It was clear from the analysis of individual samples that *Hydrobia* was extremely patchy, and the averaging of samples probably gave a misleading impression of its real distribution. It seems, however, that *Hydrobia* occurred in only relatively small numbers (below 1,000 per m²) at the lowest level along Transect 2, and also at the lowest station in Transect 4, where the density did not exceed 450 per m² except for one dense patch of some 10,000 individuals recorded in November 1943. Similarly, the lowest level along Transect 1 showed a lower

Table VIII

The changes in total population at the 14 stations. Two stations (Tr. 2, St. 4 and Tr. 4, St. 3) were not properly sampled in Nov. 1945. The autumn totals show these stations included (figures in brackets), and also excluded (figures unbracketed). (Populations to nearest hundred per m²)

Station	*Autumn Populations*			*Nov. '43–Nov. '45 % Change*	*Summer Populations*			*July '44–July '46 % Change*
	Nov. '43	*Nov. '44*	*Nov. '45*		*July '44*	*July '45*	*July '46*	
Transect 1:								
1	8,500	8,200	26,400	+211	7,500	15,000	12,800	+71
2	11,800	11,400	13,600	+15	4,200	12,300	12,500	+200
3	3,000	6,000	27,500	+817	5,000	1,900	4,500	−10
Transect 2:								
1	14,700	11,000	10,300	−30	21,900	5,200	7,800	−64
2	21,600	23,300	27,800	+29	15,200	17,900	15,800	+4
3	30,400	9,500	13,400	−56	11,600	7,200	3,800	−67
4	1,700	300	(?)300	−82(?)	1,400	3,100	3,300	+136
Transect 3:								
1	11,100	20,800	13,200	+19	13,700	14,000	5,900	−57
2	14,900	28,000	22,500	+51	13,400	14,600	7,100	−47
3	23,000	18,000	22,100	−4	16,800	12,900	11,200	−33
4	13,800	12,400	39,400	+186	12,700	5,700	4,900	−61
Transect 4:								
1	16,700	20,900	21,900	+31	10,100	18,600	23,200	+130
2	17,000	10,600	22,400	+32	7,400	8,200	6,700	−9
3	11,000	2,800	(?)1,100	−90(?)	3,800	2,000	2,200	−42
Total	(199,200) 186,500	(183,200) 180,100	(261,900) 260,500	(+31) +40	144,700	138,600	121,700	−16

Table IX

Changes in density of the main constituents of the fauna at the 14 *regular stations.* (*All numbers per m²*)

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Transect 1 *Station* 1						
Large Bivalves	80	128	52	72	28	136
Small Bivalves	88	127	127	212	127	84
Hydrobia	6,256	4,961	5,809	9,921	14,289	9,921
Chironomids	788	890	339	1,950	9,286	2,078
Oligochaetes	960	890	1,272	2,502	1,993	382
Crustacea	44	127	—	—	42	85
Polychaetes	212	340	297	42	126	—
Other Organisms	52	—	254	297	509	84
Totals	8,480	7,463	8,150	14,996	26,400	12,770
Transect 1 *Station* 2						
Large Bivalves	108	48	36	80	152	88
Small Bivalves	24	254	42	84	85	466
Hydrobia	9,472	2,120	7,208	6,233	10,939	11,872
Chironomids	792	—	1,696	3,434	1,060	—
Oligochaetes	220	339	254	636	382	—
Crustacea	20	—	—	—	85	—
Polychaetes	804	1,356	1,865	1,398	467	42
Other Organisms	372	42	296	466	381	—
Totals	11,812	4,159	11,397	12,331	13,551	12,468
Transect 1 *Station* 3						
Large Bivalves	240	36	28	12	56	454
Small Bivalves	176	255	127	127	6,275	85
Hydrobia	596	4,586	5,427	1,102	20,267	3,689
Chironomids	1,076	—	—	127	42	—
Oligochaetes	492	—	—	—	—	—
Crustacea	48	—	—	42	—	—
Polychaetes	260	128	382	508	679	212
Other Organisms	108	—	4	—	169	42
Totals	2,996	5,005	5,968	1,918	27,488	4,482
Transect 2 *Station* 1						
Large Bivalves	—	48	—	—	—	16
Small Bivalves	—	42	—	—	42	—
Hydrobia	3,567	10,685	6,190	4,282	6,402	5,003
Chironomids	127	42	—	—	—	—
Oligochaetes	10,192	9,286	3,010	127	42	297
Crustacea	—	—	42	—	—	42
Polychaetes	764	1,102	764	806	509	340
Other Organisms	—	678	1,017	—	3,265	2,247
Totals	14,650	21,883	11,023	5,215	10,260	7,945
Transect 2 *Station* 2						
Large Bivalves	56	152	140	140	196	138
Small Bivalves	84	339	212	170	212	212
Hydrobia	3,689	11,194	13,653	11,406	9,625	9,286
Chironomids	1,866	1,653	1,145	85	2,968	1,102
Oligochaetes	15,264	1,569	7,378	4,706	13,907	4,155
Crustacea	169	42	84	126	—	127
Polychaetes	466	255	339	1,059	678	84
Other Organisms	—	—	338	254	254	636
Totals	21,594	15,204	23,289	17,946	27,840	15,740

Table IX (cont.)

Transect 2 Station 3

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	32	64	16	40	80	210
Small Bivalves	212?	127	296	85	1,865	42
Hydrobia	26,966	10,770	4,918	3,307	9,922	2,671
Chironomids	1,484	85	1,654	1,272	636	339
Oligochaetes	1,145	—	339	297	424	42
Crustacea	—	—	42	42	85	212
Polychaetes	169	423	1,822	1,484	253	169
Other Organisms	423	84	382	721	169	85
Totals	30,431	11,553	9,469	7,248	13,434	3,770

Transect 2 Station 4

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	—	—	4	—	—	28
Small Bivalves	127	84	42	85	16	170
Hydrobia	678	382	85	42	48	466
Chironomids	—	—	—	—	—	1,060
Oligochaetes	—	85	—	—	—	127
Crustacea	42	—	—	170	16	127
Polychaetes	763	805	127	2,801	208	297
Other Organisms	42	—	52	—	—	1,059
Totals	1,652	1,356	310	3,098	288	3,334

Transect 3 Station 1

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	211?	100	164	76	52	26
Small Bivalves	170	127	169	42	127	42
Hydrobia	7,036	11,321	18,276	11,787	10,515	4,622
Chironomids	678	1,103	636	254	1,738	85
Oligochaetes	2,078	806	297	1,230	382	763
Crustacea	297	—	296	42	—	42
Polychaetes	635	253	296	594	296	296
Other Organisms	—	—	636	—	127	—
Totals	11,105	13,710	20,770	14,025	13,237	5,876

Transect 3 Station 2

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	140	136	64	24	84	58
Small Bivalves	42	42	212	211	423	212
Hydrobia	12,126	11,999	26,627	12,762	16,070	6,614
Chironomids	1,357	297	—	170	5,173	—
Oligochaetes	636	339	127	170	678	—
Crustacea	127	84	—	42	—	—
Polychaetes	423	424	933	1,100	—	42
Other Organisms	42	42	—	84	42	169
Totals	14,893	13,363	27,963	14,563	22,470	7,095

Transect 3 Station 3

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	84	80	32	76	132	98
Small Bivalves	64	339	338	296	552	42
Hydrobia	21,212	15,264	17,087	11,575	20,818	10,939
Chironomids	191	—	—	254	—	42
Oligochaetes	701	212	42	—	42	—
Crustacea	—	—	42	85	—	42
Polychaetes	573	762	211	381	212	85
Other Organisms	191	169	212	212	339	—
Totals	23,016	16,826	17,964	12,879	22,095	11,248

Table IX (cont.)

	Nov. '43	July '44	Nov. '44	July '45	Nov. '45	July '46
		Transect 3	*Station 4*			
Large Bivalves	128?	44	56	40	792	338
Small Bivalves	509	128?	255	169	2,586	296
Hydrobia	11,530	12,358	10,049	4,664	34,344	3,816
Chironomids	64	—	890	—	212	42
Oligochaetes	382	—	212	85	127	—
Crustacea	192	64	255	127	381	254
Polychaetes	955	128	551	593	636	169
Other Organisms	—	—	84	42	339	—
Totals	13,760	12,722	12,352	5,720	39,417	4,915
		Transect 4	*Station 1*			
Large Bivalves	127?	48	12	40	108	62
Small Bivalves	84	212	933	1,187	1,018	—
Hydrobia	12,762	7,632	18,656	15,688	20,098	22,642
Chironomids	1,187	382	—	42	—	127
Oligochaetes	933	212	127	127	—	42
Crustacea	678	—	—	42	—	42
Polychaetes	889	1,611	1,145	1,357	424	296
Other Organisms	42	—	42	84	212	—
Totals	16,702	10,097	20,915	18,567	21,860	23,211
		Transect 4	*Station 2*			
Large Bivalves	212?	20	8	12	128	4
Small Bivalves	339	2,459	297	85	1,483	85
Hydrobia	15,137	3,265	7,674	4,664	19,122	5,724
Chironomids	—	—	—	85	254	42
Oligochaetes	297	42	127	42	42	—
Crustacea	42	42	—	212	—	381
Polychaetes	1,018	1,315	2,336	3,053	1,399	423
Other Organisms	—	212	127	42	—	—
Totals	17,045	7,355	10,569	8,195	22,428	6,659
		Transect 4	*Station 3*			
Large Bivalves	126?	16	8	—	16	96
Small Bivalves	170	1,314	212	127	80	64
Hydrobia	10,049	424	339	254	160	191
Chironomids	—	—	—	—	—	191
Oligochaetes	212	—	85	42	16	—
Crustacea	42	42	84	—	176	64
Polychaetes	382	1,994	2,035	1,611	688	1,529
Other Organisms	—	42	42	—	—	64
Totals	10,981	3,832	2,805	2,034	1,136	2,199

population than along the rest of the transect, except for one particularly dense patch of 20,000 individuals per m² in November 1945. On the other hand, the lowest station along Transect 3 had a population almost as great as at higher levels, and the population was maintained over the period investigated. There is an indication that Transect 4 exhibited a slightly different distribution from the other transects in that the highest density of *Hydrobia* occurred at the uppermost level, and the population fell off sharply on passing down the shore (Table VII).

CHANGES IN THE POPULATION

The great majority of the stations showed a decline in total population from November 1943 to the following July (Table VIII). This decrease affected most of the members of the fauna (Table IX). The *total* average population in November 1944 was almost identical with that of the previous autumn, but July 1945 showed a decline again.

The counts for November 1943 are not entirely reliable, as the sampling method was still being worked out then. Nevertheless, the order of magnitude of the population is probably correct, and it is important, since that population represents a pre-fertilization autumn density for the North Bay area. Probably the data for July 1944 can also be taken as approximating to a summer *pre-fertilization* density, since, although fertilization began over Kyle Scotnish early in 1944, little effect may be expected for some months (cf. RAYMONT, 1947). In November 1945 the density increased to a relatively high level, but once more declined in the following summer, when there was a particularly marked drop (Tables IV, VIII and IX). In all three years therefore the July population was smaller than in the previous autumn.

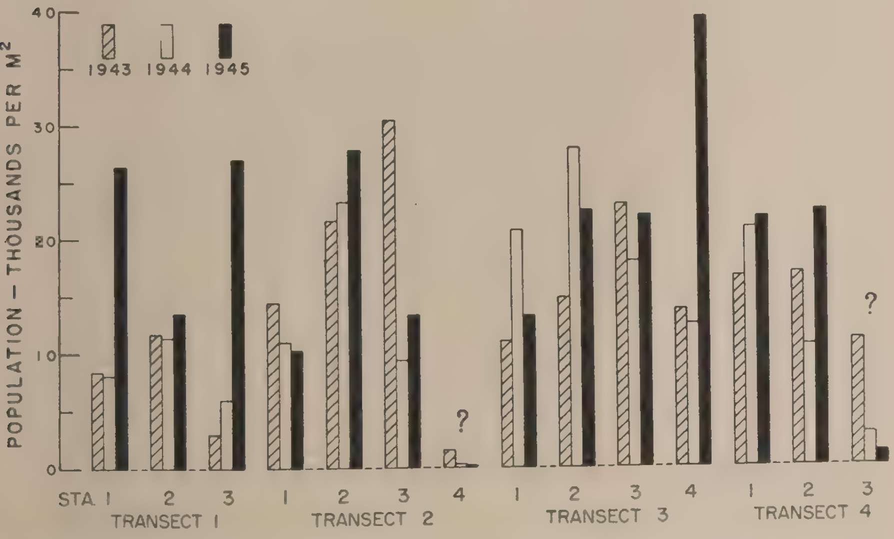

Fig. 3. A comparison of the total populations in November 1943, 1944 and 1945 at each of the 14 regular sampling stations. (Numbers per m².) (The figures at Tr. 2, St. 4 and Tr. 4, St. 3 are doubtful owing to imperfect sampling)

In considering the changes at individual stations it is probably necessary to omit Transect 2, St. 4, and Transect 4, St. 3, since on some occasions the samples could be obtained only by a grab. Of the remaining twelve stations, nine show an increase in population in November 1945 as compared with November 1943 (pre-fertilization), and two stations a decrease (Table VIII; Fig. 3). Owing to the patchiness of the fauna and to sampling errors, small differences (e.g. Transect 1, St. 2; Transect 3, St. 3) should probably be disregarded. If changes exceeding ±30% be regarded as significant, six stations showed a real increase in population—three being really large, while only one station showed a significant decline.

If the July populations are now considered, from Summer 1944 to Summer 1945 there is no obvious change. The total populations when averaged differ by only 4%, and of the individual 14 stations four only show a real increase and five a decrease.

The decline in bottom fauna densities which appeared in every July sampling seems to be more obvious in the summer of 1946. If the population then is compared with that of July 1944, the average population shows a decline, and seven stations show significant decreases as against four showing increases (Tables IV and VIII). Although it is questionable whether a decline of some 16% in the average population from July 1944 to July 1946 is significant, it is at least obvious that the changes in summer population do not parallel those of the autumn.

SIZE DISTRIBUTION OF SOME BIVALVES

An approximate picture of the size distribution of the four common bivalves in North Bay has been obtained. It is likely that, especially where very few small bivalves were taken, the combining of data obtained by the two sampling methods increases

Table X

The size-frequencies of Macoma balthica *in North Bay. The figures are averages per m² based on* 10 *sampling stations.* (*Tr.* 1, *Sts.* 1, 2 *and* 3; *Tr.* 2, *Sts.* 2 *and* 3; *Tr.* 3, *Sts.* 1, 2 *and* 3; *Tr.* 4, *Sts.* 1 *and* 2)*

Size Groups (mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
July 1944	—	6·5	8	13	4	17	13	19	30	5	5	6	3	2	0·5	0·5
Nov. 1944	4	8·5	8	13	34	13	8	25	30	1	—	3	1	2	0·5	—
July 1945	13	25	13	8	8	0·5	—	13	8	2	2	5	3	2	2	—
Nov. 1945	—	—	8·5	4	8	13	8	8	21	2	5	8	8	3	2	0·5
July 1946	—	—	—	—	—	—	4	4	21	—	—	—	—	—	—	1

Table XI

The size-frequencies of Scrobicularia plana *in North Bay. The figures are averages per m² based on* 6 *stations.* (*Tr.* 1, *Sts.* 1 *and* 2; *Tr.* 2, *St.* 2; *Tr.* 3, *Sts.* 1, 2 *and* 3). *The columns on the right of the table show the size-frequencies of small* Scrobicularia (<10 *mm*) *

Size Groups (mm)	1–3	4–6	7–9	10–12	13–15	16–18	19–21	22–24	25–27	28–30	31–33	34–36	37–39	40–42	43–45	46–48	49–51	(*mm*) 1	2	3	4	5	6	7	8	9	10
July '44	28	14	—	1	3	2	1	5	3	14	15	18	5	1	—	—	—	—	7	21	7	7	—	—	—	—	—
Nov. '44	7	28	—	1	1	1	4	5	11	13	15	9	1	1	1	1	—	—	—	7	—	14	14	—	—	—	—
July '45	28	14	49	8	5	6	2	—	7	7	7	7	3	1	1	—	—	—	21	7	—	7	7	21	21	7	—
Nov. '45	—	14	35	1	8	10	6	4	5	9	7	11	1	1	5	2	—	—	—	—	—	—	14	21	7	7	—
July '46	—	—	42	—	4	9	13	10	3	4	5	7	7	2	—	—	—	—	—	—	—	—	—	—	14	28	—

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* Data for November 1943 omitted as sampling methods then not strictly comparable with later samples.

unduly the proportion of the smaller ones, and thus at 10 mm there may tend to be an artificially sharp break in the distribution pattern. Some confirmation of this, for example, was obtained for the distribution of *Mytilus* in November 1945 (Table XII) when some quadrat counts were also made of small bivalves. Nevertheless a fair indication of the general pattern of the size distribution has been obtained (Tables X, XI, XII, XIII). The growth rates have been based on an examination of modal lengths; the use of growth rings was attempted, but numerous " false rings " interfered with the analysis.

Table XII

The size-frequencies of Mytilus edulis *in North Bay. The figures are averages per m² based on* 6 *stations.* (*Tr.* 1, *St.* 3; *Tr.* 2, *St.* 3; *Tr.* 3, *Sts.* 3 *and* 4; *Tr.* 4, *Sts.* 2 *and* 3) *

Size Groups (mm)	1–3	4–6	7–9	10–12	13–15	16–18	19–21	22–24	25–27	28–30	31–33	34–36
July '44	75	11	7	—	—	1	0·5	0·5	—	0·5	—	0·5
Nov. '44	—	7	21	—	—	—	—	—	—	—	—	—
July '45	35	21	—	—	—	—	—	—	—	—	—	—
Nov. '45	21	168	294	87	36	13	0·5	—	—	1	1	0·5
July '46	—	7	7	15	14	15	20	20	20	16	15	11

Size Groups (mm)	37–39	40–42	43–45	46–48	49–51	52–54	55–57	58–60	61–63	64–66	67–69
July '44	0·5	0·5	—	—	—	—	1	0·5	—	—	—
Nov. '44	—	—	—	—	—	—	—	—	—	—	—
July '45	—	—	—	—	—	—	—	—	—	—	—
Nov. '45	0·5	—	—	—	—	—	—	—	—	—	—
July '46	4	4	2	1	0·5	0·5	0·5	1	0·5	0·5	0·5

Table XIII

The size-frequencies of Cardium edule *in North Bay. The figures are averages per m² based on* 6 *stations.* (*Tr.* 1, *St.* 3; *Tr.* 2, *St.* 3; *Tr.* 3, *Sts.* 3 *and* 4; *Tr.* 4, *Sts.* 1 *and* 2). *Note: Up to* 10 *mm length the groups are* 3·5 *mm; thereafter* 4 *mm groupings are used**

Size Groups (mm)	1–3·5	4–6·5	7–9·5	10–13	14–17	18–21	22–25	26–29	30–33	34–37	38–41	42–45	46–49	50–53
July '44	441	42	—	4	1	4	2	2	3	3	3	—	—	3
Nov. '44	98	63	14	1·5	4	2	5·5	2	1·5	2	0·5	0·5	—	—
July '45	52	52	—	1·5	—	1	0·5	0·5	1	1·5	1	—	—	—
Nov. '45	996	396	36	11·5	1	2·5	1·5	5	3·5	2	—	—	—	—
July '46	14	28	35	1	11·5	4·5	7	3	3	1	1	—	0·5	—

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* Data for November 1943 omitted as sampling methods then not strictly comparable with later samples.

As regards *Macoma*, almost all individuals were less than 15 mm. The July 1944 and July 1945 collections suggest that young bivalves, less than one year old (O-Group), were about 2–4 mm long (Table X). The November figures indicate a growth to about 5–6 mm, but the distributions for July in each year also suggest another peak at about 8–9 mm. It is suggested therefore that this would represent approximately one year of growth. On this hypothesis there would appear to be little growth from July to the following November, since each autumn has a fairly clear peak at 9 mm. The numbers of *Macoma* larger than 10 mm is very small indeed, but those between 11 and 15 mm may be regarded as in their second year of growth. In summer 1946 there was no successful spatfall. A very few *Macoma* of about 9 mm length (presumably 1 year old) persisted, but all other age groups had disappeared (Table X).

Scrobicularia, though never very numerous, grew to a considerable size in North Bay, a proportion reaching 40 mm (Table XI). In July 1944 and 1945 a new brood of *Scrobicularia* appeared only a few mm long but (as for *Macoma*) no successful spatfall occurred in summer 1946. A difficulty is that in July 1945 the smallest *Scrobicularia* included many of 2–3 mm, but also a large number about 8 mm. When the smallest bivalves (less than 10 mm) are separated into 1 mm groups, it appears that the 2–3 mm individuals were O-Group *Scrobicularia*, and that the 8 mm individuals were probably an older group (Table XI). By November 1944 O-Group *Scrobicularia* reached a length of some 5–7 mm, and the group of 7–9 mm in the following July would presumably be one-year-old bivalves (Table XI). Thus the spat of 1944 reached about 7–9 mm by July 1945, and possibly this was the same year group which attained some 16 mm length by the following November, and about 20 mm by the next July (1946), when they would have been two years old (Table XI). If this is a true interpretation, there was some acceleration in growth rate late in 1945 and during 1946. This could well be a result of fertilization of Kyle Scotnish; the general bottom fauna in the loch did not begin to increase clearly until late 1945 (cf. RAYMONT, 1950).

As regards *Mytilus*, only the lower stations showed an appreciable population and even there mussels, especially large individuals, were extremely sparse until November 1945, when a marked increase appeared. The population then consisted mainly of small individuals, the spat of the previous summer. July 1945 figures, however, showed that very little spat had settled by that time. GAULD (private communication) observed very heavy spatfalls of *Mytilus* over the North Bay area somewhat later in that summer. Some random samplings made in collaboration with Dr. GAULD showed parts of North Bay where tremendously dense patches (even $>100{,}000$ per m^2) of very small mussels were present. Measurements on some of these collections in August and September showed the great majority of these mussels were below 5 mm—clearly the summer's spat (cf. also Table VI). Although a very large percentage of this spatfall died off very rapidly, by November 1945 a considerable population of young mussels was still present. By the following July the population had declined markedly (Table XII).

Comparison of the three July samplings shows that little spat had settled by that time each summer (Table XII). The somewhat higher figure for July 1944 may indicate a slightly earlier spatfall in that year. The 1944 brood grew to about 8 mm by November, but thereafter they disappeared (Table XII). It is possible that as they grew larger they became smothered in the soft mud substratum. Frost may also have killed them off during the winter.

The abundant 1945 spat which appeared in August and September, mostly <5 mm length, attained a length by November 1945 of approximately 9 mm (Table XII). By July 1946, although no new spat had settled, the mussels had definitely established themselves over a considerable part of the shore. Their densities had declined with winter mortality, but there was a fairly rich group ranging from 10 to 35 mm (Table XII). The mode of this group appears to be about 23 mm, and this suggests that the

9 mm peak of November 1945 has now shifted to the 23 mm peak of July 1946. This successful 1945 brood would therefore appear to have grown more than 20 mm in approximately one year. The growth rate is higher than that suggested for *Macoma* and for *Scrobicularia*, but an acceleration was suggested in the growth of *Scrobicularia* over the same period. The success of the 1945 brood of *Mytilus* and the considerable degree of colonization of the North Bay may be due in part to the general rise in productivity with fertilization noted at that time (RAYMONT, 1950).

For *Cardium*, an early spatfall occurred in summer 1944, the majority of cockles in July being about 2 mm. As for *Mytilus*, the population of *Cardium* of more than 10 mm length was generally extremely sparse over North Bay in 1944–45 (Table XIII). It would appear therefore that 1944 was an early spat year but that the brood was unsuccessful.

In 1945, spat was more abundant in the November samples than in July, indicating that the majority of the summer brood had not settled by mid-summer. *Cardium* also followed *Mytilus* in that 1945 appeared to be a much more successful year; over 1,000 small cockles per m² had settled by November 1945. All these were less than 10 mm length, and the great majority were in the smallest length class (1–3·5 mm) (Table XIII). A few cockles occurred at this time in the 10–13 mm group, and these may represent a few individuals of the I-Group, i.e. those which had settled in the previous July. By July 1946 a very heavy mortality had occurred, and there was no real spatfall. There was, however, for the first time, some indication of a spread of the somewhat larger cockles (14–25 mm) which probably represented the spat of the previous summer. The numbers, although small, suggest a fairly sharp break in the size distribution between 10 and 13 mm (Table XIII). The numbers of cockles between 10 and 28 mm taken from all six stations added together were:

10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	(Length (mm))
0	0	2	4	20	16	24	8	8	6	8	2	2	8	6	5	2	3	3	(No. per m²)

This suggests a modal length of about 14–16 mm, indicating a fairly successful brood from the previous summer (1945) which has averaged 15 mm growth in a year. This growth would be an improvement on that for *Macoma* and *Scrobicularia*, but it was not as rapid as that of *Mytilus*.

There is undoubtedly a considerable degree of overlap between this brood and an older age group (20–28 mm). A second peak possibly occurs about 23–24 mm, and this would therefore represent a two year old group of *Cardium*. The very low figures for July 1944 might also indicate one group of cockles varying in size from 18–21 mm (II-Group) and another group of 10–13 mm (I-Group). An enhanced growth rate in 1945 would agree with the results on other lamellibranchs.

It seems clear that 1945 was a fairly successful year for both *Cardium* and *Mytilus*, and that some spread of these bivalves occurred over the North Bay. Although part of the success of the 1945 brood may be correlated with better feeding conditions due to fertilization, the bivalves still experienced the difficulty of establishing themselves for any length of time on a muddy shore, subject to prolonged exposure.

DISCUSSION

The fauna of North Bay is a *Macoma balthica* community, and corresponds well to that studied by SMIDT (1951) in the Danish waddens. The polychaete and lamellibranch species of the infauna are very similar, with *Hydrobia ulvae* as the dominant gastropod. SMIDT quotes *Mytilus edulis* and *Littorina littorea* as the two most important members of the epifauna—a composition that accords well with the North Bay mud flat. One marked difference was the very low numbers of *Corophium* found in North Bay. THAMDRUP (1935), SMIDT (1951), BEANLAND (1940), SPOONER and MOORE (1940) all quote this species as an important member of the *Macoma* community. BEANLAND, and SPOONER and MOORE, suggest that one factor which limits its occurrence is lack of shelter, so that its maximum density is usually near high-water mark. Nevertheless *Corophium* might have been expected to occur abundantly at least at the higher levels of North Bay, which is at the end of a long, sheltered sea-loch. Moreover, *Hydrobia*, which is also said to be sensitive to water movement, was very abundant—in fact dominant numerically—in North Bay. There have been some suggestions that *Corophium* may occur only as a temporary visitor on shore; perhaps sampling only in July and November missed its abundant season. Possibly also *Corophium* competes with other members of the fauna that were plentiful in North Bay (cf. THAMDRUP, 1935).

Another difference between other described *Macoma* communities and North Bay was the importance of chironomid larvae in the latter area. These larvae are not mentioned by THAMDRUP (1935), SMIDT (1951), FRASER (1932), BRADY (1943) or REES (1940). SPOONER and MOORE (1940) do list " dipterous larvae " on a few occasions in their tables, but the numbers are very low, and clearly if there were Chironomidae, they were never of importance. WOHLENBERG (1937) also mentions chironomid larvae in a small area near a fresh water stream, but they did not apparently occur generally over the mud flat. NICOL (1935) found high densities (maximum 39,000 per m^2) in muddy salt pools. Over the North Bay the average population varied between 300 and 1,500 per m^2 from 1943 to 1946, but individual samples gave densities of 2,000–3,000 per m^2 (maximum $>$9,000 per m^2).

Oligochaetes (chiefly *Peloscolex*) were also very abundant in North Bay; the average population for the shore ranged near 1,000 per m^2 for a considerable period, and individual samples amounted sometimes to several thousands (maximum 13,900 per m^2). SMIDT (1951) comments on Oligochaeta (including *Peloscolex benedeni*) as being exceedingly numerous on the higher parts of the waddens, and BRADY (1943) found they occurred in muds off the Northumberland coast, though the densities in North Bay were very much higher. *Peloscolex* was also found by WOHLENBERG (1937).

Most authors state that *Hydrobia* is concentrated in the upper tidal areas (cf. SPOONER and MOORE); in North Bay the lowest stations usually had few. However REES (1940) found it in greater density towards low water, and SMIDT states that the young *Hydrobia* occurred in great numbers in summer and autumn anywhere over the mud flats. This could account for the very dense patches occasionally encountered in North Bay, even at the lowest tidal levels (cf. p. 185). The maximum densities recorded by most workers in Great Britain do not usually exceed 20,000 per m^2 (Table XIV); though NICOL (1935) found up to 32,000 per m^2 at Aberlady, Scotland. The richness of North Bay is therefore apparent. However, the densities there were not as high as those at Skalling (Table XIV). SMIDT (1951) recorded even higher densities for the Danish waddens when O-Group *Hydrobia* were also counted (Maximum 600,000 per m^2).

Of the bivalves typical of the *Macoma* community, *Mya* was taken only rarely in North Bay. *Macoma* seemed able to live over a very broad zone of the shore, though the lowest station of Transects 2 and 4 was quite definitely avoided—*Macoma* occurred only once there during the whole period of sampling. The density of *Macoma*, even in comparatively rich zones, appears rarely to exceed 200–300 per m², and North Bay would therefore be quite a dense area. However, THAMDRUP recorded up to 1,000 per m² at Skalling, and FRASER far higher densities in the Mersey Estuary (Table XIV).

In general the great majority of individuals in the higher counts in North Bay were young (<10 mm); a particularly striking example was the maximum count of 428 per m² of which only four exceeded 10 mm. Densities of individuals >10 mm rarely rose to 60 per m². WOHLENBERG (1937) found $>6{,}000$ O-Group *Macoma* at Sylt. Similarly the 6,300 individuals per m² recorded at Skalling (Table XIV) were all young. SMIDT found even 16,000 O-Group *Macoma* per m² in the same area, though he also showed that the stock was reduced to some hundreds per m² in a few months.

STEPHEN (1931) believes that *Macoma* breeds about April–May, young individuals appearing by June and reaching a length of some 5 mm by the end of their first autumn. By the end of their second autumn, STEPHEN found an average length of 8–9 mm, and he believes that a heavy mortality occurs after the third summer. The growth rate of *Macoma* in North Bay would seem to parallel closely STEPHEN's results. Young spat, 2–4 mm, appeared in the July samplings and reached about 5–6 mm by the first autumn (November) and some 9 mm by the following autumn. The conditions for growth in North Bay would appear to be favourable. BRADY (1943), for collections in June, gives an average length of 6 mm for I-Group and 12 mm for II-Group *Macoma*.

THAMDRUP (1935) records *Scrobicularia* at the lower levels at Skalling. SMIDT and WOHLENBERG found it occasionally in soft deposits, and STEPHEN (1930) records it in soft sticky mud in the Firth of Forth. In North Bay this bivalve was widespread in the soft substratum, though it definitely avoided the lowest tidal levels. Thus it was never taken at the lowest station in Transect 2, only once at the lowest station of Transects 1 and 4, and only twice at the lowest station in Transect 3. SPOONER and MOORE (1940) also indicate that *Scrobicularia* is commoner in the upper half of the inter-tidal zone. Except for one extraordinarily dense patch of 1,000 per m² recorded by SPOONER and MOORE (1940), the densities of *Scrobicularia* would not appear to exceed 300 per m² (Table XIV). SPOONER and MOORE describe the Tamar as a rich *Scrobicularia* area, and they regard this species as generally abundant in sheltered inter-tidal areas in the South of England (cf. also HOLME, 1949). It would appear that North Bay was at least equally rich (Table XIV). The higher densities recorded by SPOONER and MOORE showed a high proportion of young spat. This was also true of the North Bay samples, but counts of 100–150 larger individuals per m² were quite common. SPOONER and MOORE do not give details of growth rates, but they remark that specimens <12 mm in length include both O-Group and I-Group. This would agree reasonably with the suggestion (p. 192) that in North Bay *Scrobicularia* grew to about 6 mm by the end of their first autumn, to about 8 mm by the following July, and to some 16 mm by the end of the second autumn when some acceleration is postulated.

SPOONER and MOORE have suggested that *Macoma* and *Scrobicularia* may compete, since they seem to have similar feeding habits. The population of *Scrobicularia* in North Bay, while not very large, was about as rich as that of the Tamar Estuary, and possibly therefore *Macoma* was to some extent excluded from North Bay.

Cockles were not very common in North Bay; the density of older individuals never exceeded 80 per m^2. The much higher figures occasionally recorded showed without exception an overwhelming dominance of young cockles ($<$ 10 mm). The densities do not, however, compare unfavourably with those for other areas in Britain, especially as the high populations recorded by STEPHEN and by SPOONER and MOORE were composed mainly of O-Group cockles. By contrast, THAMDRUP found very much higher densities at Skalling (Table XIV); indeed *Cardium* was the most abundant bivalve on the waddens. The maximum quoted even then (4,675) did not take account of O-Group individuals. THAMDRUP showed that several thousand O-Group per m^2 also occurred, but that the densities declined rapidly during autumn and winter. SMIDT and also WOHLENBERG found even larger settlements of O-Group cockles: SMIDT found 20,000 to 30,000 per m^2 quite frequently, and WOHLENBERG recorded some 40,000 per m^2, but he also showed how rapidly those numbers were reduced.

Table XIV

Comparison of the densities of some of the members of the fauna in North Bay and in other areas. Numbers are maximal densities per m^2. Figures in brackets indicate extraordinarily high densities recorded only once

Locality	Tamar	Exe	Bristol Channel	Forth and Clyde	Northumberland	Skalling	Mersey	North Bay
Authority	SPOONER and MOORE (1940)	HOLME (1949)	REES (1940)	STEPHEN (1929, 1930, 1931, 1932)	BRADY (1943)	THAMDRUP (1935)	FRASER (1932)	RAYMONT (this paper)
Hydrobia	10,000–14,000 (28,000)	16,000	18,000	1,400 (3,000)*	—	15,000–46,000 (60,000)	—	10,000–26,000 (34,000)
Macoma	36 (76)	20–30	800	150–200	150–220 (554)	300–1,000 (6,300)	2,000–5,000 (5,900)	250 (428)
Scrobicularia	100–280 (1,000)	230	—	136	—	20–60	—	150–330
Cardium	100–200 (383)	200	—	100–150 (300)	50–160 (192)	2,000–3,000 (4,675)	64	1,000 (6,000)
Pygospio	—	2,540	—	—	—	14,000–20,000	—	2,840
Heteromastus	60–90	—	—	—	—	10–40	—	1,400 (1,740)
Arenicola	3	50–60	—	16 (76)*	40–60	100	—	200–380 (470)
Nereis	1,000 (>3,000)	20 (130)	2,000	110 (396)†	25	100–320	‡	600–700 (890)
Nephthys	100–300 (500)	100	—	36	50–60	90	—	100–210

* = Loch Gilp, Scotland. † = Isle of Barra, Scotland. ‡ = " abundant ", no density quoted.

STEPHEN (1931) concluded that *Cardium* bred in summer at Millport, the smallest cockles appearing about August and reaching a length of $<$6 mm by the end of their first autumn. By the following July these cockles reached 12–13 mm. BRADY (1943) states that in June one-year-old cockles had an average length of 11 mm, and SMIDT (1951) shows in July one-year-old cockles reaching a length of 12 mm, or about 16 mm in a favourable year.

The results of the North Bay collections, and also the results from Loch Craiglin (RAYMONT, 1947) strongly support STEPHEN'S view that *Cardium* spawns in summer, but the growth of the cockles up to November in North Bay was somewhat less than STEPHEN found. However, the 1945 spat attained a length of about 15 mm in North

Bay by July 1946, i.e. their growth was of the same order as that given by Stephen and Brady, and (in a favourable year) by Smidt. This improvement may reflect the better feeding conditions in North Bay in 1945/46.

The density of *Mytilus* was usually very low over the whole of North Bay, the only heavy settlements being at spatfall (August), after which the animals did not come into the regular samplings. Chipperfield (1953) shows that April May is the most likely breeding time for *Mytilus* on British coasts; the period of settlement seems to be May to early July. Some authors, however, have recorded settlements in August, and this clearly was the main period for North Bay (p. 192).

Following a heavy spatfall the numbers of *Mytilus* declined very rapidly (cf. other bivalves), so that only once (July 1946) was an appreciable number of the larger mussels found (200–400 per m²). Smidt found that the Danish waddens were unsuitable for *Mytilus*; the numbers found were negligible, although on the banks very high densities of mussels occurred. Similarly Thamdrup recorded densities of 2,000–12,000 mussels per m² on the banks, while over the mud flats only an occasional mussel was taken.

The growth rate of young *Mytilus* seems to vary greatly according to conditions (cf. White, 1937; Smidt, 1951). For example, Smidt quotes other workers as stating that young spat may grow to 8 mm in less than two months if permanently covered with water, whereas similar spat, left uncovered for a few hours daily, hardly attained 4 mm in three months. White (1937) states that under unfavourable conditions a mussel may add only a few mm in a year, but under good conditions, at St. Andrews, two-year-old mussels ranged from about 30–50 mm. This would indicate a growth at least of some 15–25 mm in a year. The long exposure periods over North Bay would suggest a rather unfavourable environment; nevertheless the 1945 spat grew to 9 mm by November and to about 20 mm in the following July, when these mussels would be one year old. This approximates to the figure mentioned by White, and emphasizes that feeding conditions in 1945/46 over North Bay must have been very good.

Of the polychaetes, *Pygospio* was obviously dominant in North Bay. Wohlenberg found *Pygospio* at upper tidal levels, though in relatively low densities, but Thamdrup recorded very high densities, mainly near high water (Table XIV). Smidt, however, found that very large concentrations of newly settled *Pygospio* ($>$31,000 per m²) might occur right across the shore. In North Bay *Pygospio* was definitely more abundant at lower tidal levels, but it was so common that there was an average population for the whole mud flat of 160–580 per m² (Fig. 4). There are few records of large populations of this polychaete in Britain. However, Holme (1949) found a density for the Exe Estuary similar to that of North Bay, though the populations are far below those of Thamdrup for Skalling (Table XIV). Brady (1943) records up to 600 *Scoloplos* per m² and fairly high numbers of *Spio* and *Scolecolepis* in Northumberland muds: perhaps these polychaetes replace *Pygospio*.

Heteromastus filiformis was the next commonest polychaete in North Bay; apart from the sharp decline in July 1946, the average population was 30–290 per m² (Fig. 4). *Heteromastus* was quite sharply restricted to mid-tide levels (higher in Transect 4), and the maximal densities were considerably greater than either those recorded by Spooner and Moore for the Tamar, or by Thamdrup for Skalling, Denmark (Table XIV). However, Smidt (1951) found that in 1947 *Heteromastus* became abundant on the Danish waddens, with some dense patches of mostly young worms exceeding 2,000 per m².

The average population of *Arenicola* over North Bay varied between 30 and 70 per m², apart from the marked decline in July 1946 (Fig. 4). Densities up to 400 per m² occurred over part of the shore (Table XIV). However, *Arenicola* was absent from a considerable number of stations; possibly it was commoner above mid-tide level, but there was no clear distribution pattern. Many authors have shown that lugworms generally avoid soft substrata and live in essentially sandy bottoms. Thus in SPOONER and MOORE's work, *Arenicola* hardly ever appeared in the samples. However, in the Exe and off the Northumberland coast small populations of *Arenicola* occurred (Table XIV), and STEPHEN (1930) found a rich ground in Loch Gilp. THAMDRUP

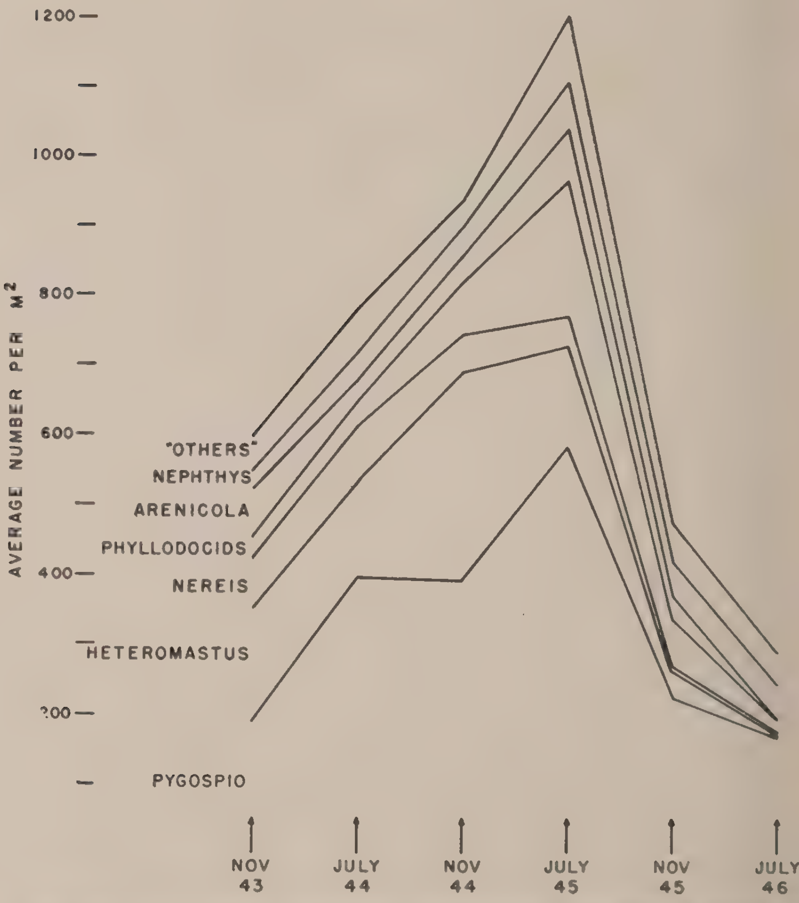

Fig. 4. Fluctuations in the density of polychaetes over North Bay. The changes in the total population and in the main species are shown. All numbers represent densities per m² calculated as averages of the populations at 14 sampling stations

found *Arenicola* fairly widely distributed at Skalling, but the densities were <35 per m², except for occasional heavier populations of young worms.

Nereis diversicolor appears to be very restricted in North Bay. Most investigators (STEPHEN, SPOONER and MOORE, BRADY, WOHLENBERG, SMIDT) have found that this species occurs abundantly only at upper tidal levels. This was true also in North Bay, but the only station where the polychaete was really abundant was Transect 2, Station 1, where densities of >800 per m² were recorded (Table XIV). At most stations in North Bay *Nereis* never appeared at any time. HOLME (1949) also found it occurred infrequently in the Exe Estuary, and BRADY's densities for Northumberland are low. STEPHEN recorded fairly small populations for the Forth and Clyde, though he did find a high density on the Isle of Barra (Table XIV). On the other hand, WOHLENBERG (1937) found *Nereis* to be abundant at Sylt, and SPOONER and MOORE (1940) found it was a very common polychaete in the Tamar muds. REES (1940) also recorded high densities for the Bristol Channel (Table XIV). THAMDRUP (1935), in contrast to most workers, did not find *Nereis diversicolor* restricted to the upper tidal zones. His maximal densities were not very large, and varied from year to year (Table XIV). However, SMIDT (1951) has recorded many thousands of young O-Group *Nereis* from the same area, though adults were few. NICOL (1935) also once recorded the extraordinary density of 95,700 *Nereis* per m² (all young) from a salt mud pool at Aberlady.

Nephthys contrasted with *Nereis* over North Bay in being fairly restricted to low tidal levels. There appears to be general agreement that *Nephthys* occurs more frequently towards low tide mark. Although *Nephthys* occurred regularly in North Bay, the numbers were never high (Fig. 4). Indeed, the densities recorded for other areas are mostly rather low. SPOONER and MOORE, however, found somewhat higher populations in the Tamar (Table XIV).

It is clear that, while the fauna of North Bay is rich, comparatively few species reach really high densities (*Hydrobia*, chironomids, *Peloscolex*). These animals, though widespread, appear to be more typical of the upper tidal zones, and were probably favoured by the long and rather irregular periods of exposure over North Bay. The total average fauna varies between 8,700 and 18,700 animals per m² (Table IV), although individual stations showed populations exceeding 25,000 per m² (maximum 39,000). By contrast, BRADY (1943) gives an average density for a Northumberland mud flat of <400 animals per m².

SMIDT (1951) gives figures (Table 21, p. 138 of his paper) for the total numbers of animals per m² for Danish shallow water areas. The extraordinary richness of the Danish waddens (30,000–60,000 per m²) is outstanding, and SMIDT attributes this mainly to the predominance of small species (*Hydrobia*, *Pygospio*, etc.), and to the young of many species. Though the average density in North Bay was not nearly so high, the fauna was rich and, like the waddens, was characterized by the abundance of small animals (*Hydrobia*, *Peloscolex*, chironomids, *Pygospio*), and by young individuals especially of molluscs. The fauna was also similar to that already described by RAYMONT (1947, 1949) for Loch Craiglin, where the total average density rose with fertilization to 16,000 and even 23,000 animals per m², and where the same species (*Hydrobia*, chironomids, young *Cardium*) were dominant.

The results of the population changes over North Bay show a pronounced seasonal fluctuation which is not unexpected in an inter-tidal area. Previous studies in Loch

Sween showed fairly clear seasonal effects, even in the bottom fauna below low-tide mark (RAYMONT, 1947, 1950). But in Loch Craiglin, and in the areas of Kyle Scotnish below low-water mark, the maximum population occurred during the summer, whereas in North Bay the populations in November were consistently larger than in July. In Loch Craiglin, however, the actual months in which the highest densities were experienced were August and September, and a few stations in the loch did show higher densities even in November. In Kyle Scotnish, too, the high " summer " peaks of the bottom fauna represented an average of the three months, July, August and September. It seems clear, as indeed might be expected in a marine area, that the high densities occurred in *late* summer or even afterwards.

It is not surprising that the July samplings should give a lower population than the November samples. Most of the young larvae produced during spring and summer will not have settled and grown to a sufficient size to appear in July samplings. For example, SMIDT (1951) found that the vast majority of *Hydrobia* in June belonged to O-Group, and measured only 0·5 mm. Since they grow only some 2 mm by the winter, it is likely that sampling with a 1 mm sieve in July would miss the majority of the brood. The strong seasonal fluctuation is in fact dominated by *Hydrobia* (Tables IV and V), but the seasonal changes hold also for chironomids, bivalves, oligochaetes and " other organisms ". Chironomids may be expected to oviposit mainly during the summer, and therefore the new larvae will hardly appear in sievings before early autumn. It has also been shown that the main spatfalls of *Cardium* and *Mytilus* occur after July. During the ensuing winter and spring there will be heavy depredations on the bottom fauna, and also the physical conditions (especially frost) over winter will cause the fauna to decline. Little recruitment may be expected before July in the following year.

The results from November 1943 to July 1945 indicated then no real change in the overall population, apart from these seasonal fluctuations. This is borne out by both the average populations (Table IV) and by the results from individual stations (Table VIII, Fig. 3). The rise in November 1945, however, was definite and widespread. The average increase was 40%, and a large number of individual stations showed a rise (Fig. 3, Table VIII).

A rise of only 40% could easily result from a " natural " fluctuation, i.e. it might be attributed to some favourable condition other than increased food supply. Wide variation in the success of year-groups of bottom animals are well known (BOYSEN-JENSEN, 1919; THAMDRUP, 1935; WOHLENBERG, 1937; STEPHEN, 1931, 1932, 1938). Nevertheless it is usual then for some species to show one particular year as a good brood year, while for other species that same year may be very poor (cf. BOYSEN-JENSEN, 1919, for species of bivalves). The fact that so many of the main constituents of the fauna over North Bay showed an increase at the same time (Table IV), lends considerable support to the view that the rise in November 1945 was due to the improved conditions resulting from fertilization. The accelerated growth rate seen in some lamellibranchs (p. 192–193) would also agree with this conclusion.

By July 1946 the average population over the North Bay had declined sharply from the previous high autumn density to reach the lowest value for the period of sampling. This marked fall may be largely explained as a seasonal change as in previous years. It is not easy, however, to account for the especially severe drop in the density of the fauna in 1946. Kyle Scotnish had been stocked with plaice fry in 1945, and a more successful stocking involving ca. 1,500,000 fry was made in the spring of 1946 (GROSS, 1950). To what extent the young flatfish fed over the mud flat at high tide it is impossible to say; nevertheless a considerable increase in the amount of food taken by the fish was inevitable, especially in view of the very high growth rate (cf. GROSS, 1950).

Possibly the drop in the fauna was also partly related to the severe frost in February and March of that year. Thus an extract from the log book states that work was impossible at the head of the loch (i.e. just off North Bay) on 28th February 1946, because of ice. The following day the whole of Kyle Scotnish was covered with ice, and this cleared from the northern parts of the loch only on 5th March. The general bottom fauna of Kyle Scotnish below low-tide mark was not severely checked by these frosts (cf. RAYMONT, 1950) but over an inter-tidal mud flat the bottom animals, except for those burrowing really deeply, would be exposed fully to the severe effects of freezing.

It is significant that almost all the fauna (*Hydrobia*, polychaetes, chironomids, oligochaetes, etc.) showed the great reduction in numbers by July 1946, i.e. it was not an unsuccessful spawning or a poor settlement by merely one important species of the community. On the other hand, the population of large bivalves remained almost stationary from November to July, and indeed the final population (125 large bivalves per m^2) was higher, except for November 1945, than at any other time (Tables IV, XII, XIII). It is these larger bivalves which can burrow away from the surface, some like *Scrobicularia* to a considerable depth, and thus escape, to some degree, adverse conditions. By contrast, the youngest bivalves were decimated over the same period, falling from more than 1,000 to 129 per m^2 (Table IV).

In the earlier years few large bivalves occurred over North Bay (Tables XII and XIII). Probably these molluscs are periodically greatly reduced in numbers by adverse conditions in the area. The lack of the older bivalves is especially true of *Mytilus* which is of course a surface dweller. By contrast, *Scrobicularia*, which burrows deeply, and as older individuals may therefore escape the worst conditions, is not so poorly represented by the older age groups (Table XI).

The only marked exception to the general seasonal fluctuations, and to the large increase in November 1945, was in the polychaete group (Fig. 4). These animals exhibited a fairly steady increase in population from November 1943 onwards, and they reached an average of 1,200 animals per m^2 in the summer of 1945, after which there was a very sharp decline to the summer of 1946 (Table IV). These changes were mainly due to *Pygospio* (Fig. 4). This polychaete was numerically dominant over the whole period November 1943 to July 1946. It also appears to have reproduced in the years 1944 and 1945 sufficiently early for there to be a sharp increase in the polychaete populations in each summer. From November 1943 to July 1944, for example, the population of *Pygospio* more than doubled, and from November 1944 to July 1945 there was an increase of 50%.

Phyllodocidae also contributed to the sharp peak in the summer of 1945 (Fig. 4). The only other polychaete that played a significant part in the overall population changes was *Heteromastus filiformis*—the second most important polychaete. During 1944 there appears to have been a successful brood of *Heteromastus*, so that between July and November of that year the population more than doubled, but the most surprising change was the very sharp decline in *Heteromastus* from July 1945, so that the population was virtually wiped out by the summer of 1946. This was also true of

Nereis diversicolor and *Arenicola marina* (Fig. 4). Not a single *Arenicola* was taken in July 1946, and *Nereis* and *Heteromastus* occurred only in one auger sample (Transect 4, St. 1), at that time. The decline in the polychaete population affected the other species also, though not quite so obviously (Fig. 4); the only exception was *Nephthys*.

The increase in *Heteromastus* and *Pygospio* in 1944, and in *Pygospio* and Phyllodocidae in the following year, may be " natural " fluctuations, though probably the increased food supply in Kyle Scotnish due to fertilization in the early years may have helped in their success. The decline in 1946, in contrast to the rise in the polychaete population below low-water mark, (RAYMONT, 1950) may be attributed to the adverse conditions over the exposed inter-tidal mud flats in the winter. It may not be without significance that *Nephthys* was the only polychaete which did not suffer the decline. This species was sharply limited to the lowest tidal limits on the shore, and it therefore would not be long exposed to freezing. Over the same period *Nephthys* was increasing, together with other polychaetes, in the areas *below* low water in Kyle Scotnish.

It would appear that fertilization, with the resulting increase in food over the North Bay area, had little lasting effect on the density of the bottom fauna. While some increase did occur when other environmental conditions were also favourable, the beneficial effect was more than wiped out by other adverse conditions, and the increase in density was at the most temporary. It is clear, therefore, that increase in food supply alone cannot compensate for other adverse features in the environment. Any attempt at fertilization in inter-tidal areas should therefore be made only in those areas where the species of animals whose increase is desired are either naturally " hardy ", or where the environmental conditions such as temperature, salinity, and so on are constantly favourable.

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REFERENCES

BEANLAND, F. L. (1940), Sand and mud communities in the Dovey Estuary. *J. Mar. Biol. Assoc., U.K.*, **24**, 589–611.

BOYSEN-JENSEN, P. (1919), Valuation of the Limfjord. I. Studies on the fish-food in the Limfjord 1909–1917. *Rept. Danish Biol. Sta.*, **26,** 1–45.

BRADY, F. (1943), The distribution of the fauna of some inter-tidal sands and muds on the Northumberland coast. *J. Anim. Ecol.*, **12,** 27–41.

CHIPPERFIELD, P. N. J. (1953), Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Assoc., U.K.*, **32,** 449–476.

FRASER, J. A. (1932), Observations on the fauna and constituents of an estuarine mud in a polluted area. *J. Mar. Biol. Assoc., U.K.*, **18,** 69–85.

GROSS, F. (1950), A fish cultivation experiment in an arm of a sea-loch. V. Fish growth in Kyle Scotnish. *Proc. Roy. Soc., Edinburgh*, B, **64,** 109–135.

HOLME, N. A. (1949), The fauna of sand and mud banks near the mouth of the Exe Estuary. *J. Mar. Biol. Assoc., U.K.*, **28,** 189–237.

NICOL, E. A. T. (1935), The ecology of a salt-marsh. *J. Mar. Biol. Assoc., U.K.*, **20,** 203–261.

RAYMONT, J. E. G. (1947), An experiment in marine fish cultivation: IV. The bottom fauna and the food of flatfishes in a fertilized sea-loch (Loch Craiglin). *Proc. Roy. Soc., Edinburgh*, B, **63,** 34–55.

RAYMONT, J. E. G. (1949), Further observations on changes in the bottom fauna of a fertilized sea-loch. *J. Mar. Biol. Assoc., U.K.*, **28,** 9–19.

RAYMONT, J. E. G. (1950), A fish cultivation experiment in an arm of a sea-loch. IV. The bottom fauna of Kyle Scotnish. *Proc. Roy. Soc., Edinburgh*, B, **64,** 65–108.

REES, C. B. (1940), A preliminary study of the ecology of a mud-flat. *J. Mar. Biol. Assoc., U.K.*, **24,** 185–199.

SMIDT, E. L. B. (1951), Animal production in the Danish Waddensea. *Medd. Komm. Danmarks Fisk. Havundersøgelser*, Ser. Fisk., **11** (6), 1–151.

SPOONER, G. M. and MOORE, H. B. (1940), The ecology of the Tamar Estuary. VI. An account of the macrofauna of the inter-tidal muds. *J. Mar. Biol. Assoc., U.K.*, **24,** 283–330.

STEPHEN, A. C. (1929), Studies on the Scottish marine fauna: The fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc., Edinburgh*, **56,** 291–306.

STEPHEN, A. C. (1930), Studies on the Scottish marine fauna: Additional observations on the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc., Edinburgh*, **56,** 521–535.

STEPHEN, A. C. (1931), Notes on the biology of certain lamellibranchs on the Scottish coast. *J. Mar. Biol. Assoc., U.K.*, **17,** 277–300.

STEPHEN, A. C. (1932), Notes on the biology of some lamellibranchs in the Clyde area. *J. Mar. Biol. Assoc., U.K.*, **18,** 51–68.

STEPHEN, A. C. (1938), Production of large broods in certain marine lamellibranchs with a possible relation to weather conditions. *J. Anim. Ecol.*, **7,** 130–143.

THAMDRUP, H. M. (1935), Beiträge zur Ökologie der Wattenfauna. *Medd. Komm. Danmarks Fisk. Havundersøgelser*, Ser. Fisk., **10** (2), 1–122.

WHITE, K. M. (1937), *Mytilus. Liverpool Mar. Biol. Comm., Mem.*, No. 31, 1–177.

WOHLENBERG, E. (1937), Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. *Helgoländer Wissensch. Meeresunters.*, **1** (1), 1–92.

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Distribution of planktonic Foraminifera in some Mediterranean sediments*

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Summary—The planktonic foraminiferal populations of the Mediterranean Sea may be differentiated from those of the adjacent Atlantic Ocean.

Three distinct populations are found located in the western and eastern Mediterranean and the Aegean Sea, and additional discrete populations may occur in the unsampled areas.

Populations probably are derived from the Atlantic and from indigenous ancestral stock.

The direction of coiling of *Globorotalia truncatulinoides* shows a shift to left coiling dominance within the Mediterranean. Additional statistical analysis may give further evidence concerning derivation of species in the area.

INTRODUCTION

The planktonic Foraminifera in sediment-surface samples from forty-six stations throughout the Mediterranean Sea have been studied and compared with planktonic assemblages in the adjacent Atlantic. These populations show some regional variation and the Mediterranean faunas as a whole differ from those of the Atlantic. The samples were collected, in 1947–48, by members of the Woods Hole Oceanographic Institution on R/V *Atlantis* Cruise 151. This study was supported by the Office of Naval Research (Project NR 081-050, Contract Nonr—233 Task 1). The drafting was done by Miss J. F. Peirson and R. R. Lankford.

Much has been published on the description and taxonomy of Mediterranean faunas but few quantitative studies have been made. Phleger (1947) gives quantitative lists of planktonic species in top samples of three long cores from the Tyrrhenian Sea, but suggests that at least one of these does not represent the modern fauna. Muraour (1954 a, b) gives quantitative data for two stations near Algiers. Di Napoli-Alliata (1952) gives a very useful résumé of the literature on Mediterranean planktonic faunas.

The stations (Fig. 1, Table I) are scattered throughout most of the area south of North Latitude 38° 51′ with the exception of four in the northern part of the Aegean Sea. No samples were obtained from the Adriatic Sea, where many of the previous studies have been made, nor from the northern part of the western Mediterranean. The samples were collected with a gravity corer or with a coring tube attached to a camera and are believed to contain material from the surface of the sediment. Three hundred to five hundred planktonic specimens larger than 0·149 mm were counted from each and the relative abundances of the species calculated. Samples having fewer specimens are omitted; the majority contain many more.

SURFACE TEMPERATURE AND SALINITY DISTRIBUTION

For convenience in the later discussion of the planktonic populations, the area may be divided into three parts: western Mediterranean, eastern Mediterranean, and the

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* Contribution No. 20, Marine Foraminifera Laboratory; Contribution No. 803, Scripps Institution of Oceanography.

Aegean Sea. The depth of the surface-water layer in the Mediterranean is approximately 200 m or less. Although planktonic Foraminifera have been found living at greater depths it is probable that they are most abundant in the upper layers (Phleger, 1954) and it is assumed here that the characteristics of the surface layer are those to which they are adapted.

The eastern and western basins of the Mediterranean are separated by a sill, between Sicily and Tunis, having a maximum depth of about 400 m. The western basin (Tyrrhenian Sea and Algiers-Provençal Basin) is separated from the Atlantic by a sill depth of 320 m. Water enters the Mediterranean from the Atlantic and passes from the western basin to the eastern basin by surface currents. In both cases water flows westward at intermediate depths. A study of numerous sources of information shows that the surface temperature variation in the western area is approximately 13° C to 24° C, the warmest season being in July-August and the coldest in February-March. Greater extremes are found at various near-shore areas, especially along the coast of France. The temperature of the surface water just east of Gibraltar in August, 1938, was 19·5° C rising to 24° C farther east (Rouch, 1940). Surface salinities vary from 36‰ at Gibraltar to 38‰ near Sicily. Variable salinities are often found at near-shore localities. In 1949-50 at Monaco there was a winter variation from 36·8‰ to 38·5‰ and at Algiers 34·5‰ to 37·6‰ (Kruger, 1950). The eastern basin (Ionian Sea and Levantine Basin) apparently contains surface water derived chiefly from the west via the surface current through the Sicily-Tunis gap. The deep water, according to Pollak (1951), is all derived from the Adriatic Sea. Little is known at present about the influence of the Suez Canal, but it is probable that any water derived from this source would quickly lose its identity. Surface temperatures in this area vary from 16° C to 24° C in the western part and 16° C to 28° C in the extreme east. Surface salinities vary from 38‰ in the west to approximately 39·5‰ in the east but here again local variations may occur near shore. An example of this is the comparatively low salinity of 30‰ found off Gaza, Israel, in September, 1947, due probably to the Nile flood (Oren, 1952). Surface currents enter the Aegean Sea from the southeast and from the Black Sea. Surface temperatures vary from 13° C to 25° C and surface salinities from approximately 30‰ near the Dardanelles to 39‰ just north of Crete. Due to the counter-clockwise surface circulation, salinities on the eatern side are higher than those on the western.

These data show that there are lower winter temperatures and somewhat lower salinities in the western than in the eastern Mediterranean. In the Aegean there are lower winter temperatures than in the eastern area and a complex salinity pattern with comparatively low salinities in the northern part.

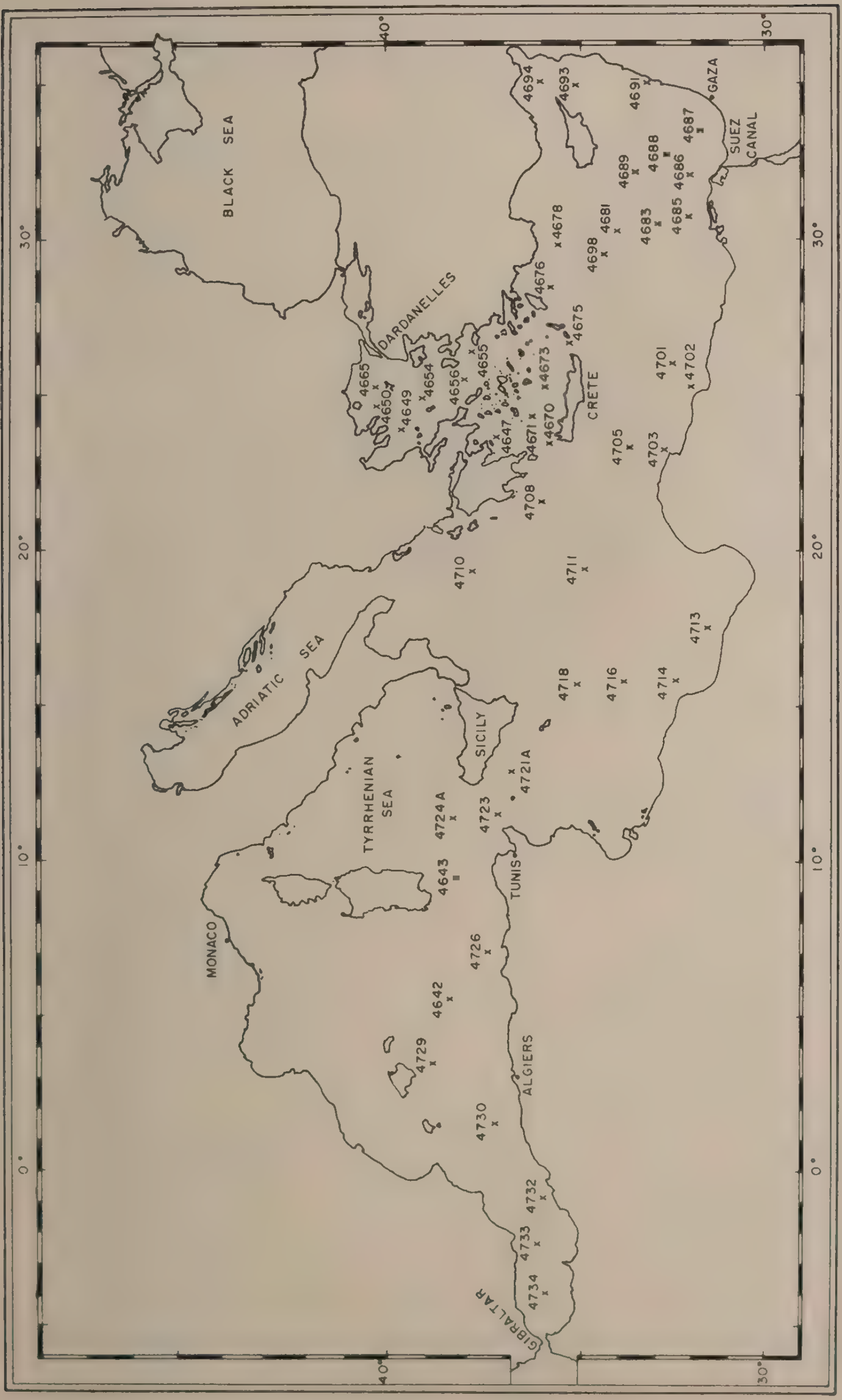
Conditions in the Atlantic immediately west of Gibraltar are also of interest. Here the surface temperature variation is somewhat less than in the Mediterranean, 16° C to 22° C. The surface salinity is somewhat less than that obtaining at Gibraltar.

DISCUSSION OF PLANKTONIC POPULATIONS

The identifications of the planktonic species are in most cases the same as those given by Phleger, Parker and Peirson (1954) in their study of Atlantic deep-sea cores. Some species groups, as defined here, contain forms recognized as species or varieties by some authors. Their omission does not necessarily indicate that they are believed to be invalid. *Globigerinoides rubra* probably includes, or in some cases is

Table I. *Percentage distribution of planktonic Foraminifera in the Mediterranean Sea and adjacent Atlantic Ocean.*

	ATL.			MEDITERRANEAN																																													
STATION	4637	4736	4735	4734	4733	4732	4730	4729	4642	4726	4643	4724A	4723	4721A	4718	4716	4714	4713	4711	4710	4708	4705	4703	4702	4701	4676	4678	4698	4681	4683	4685	4686	4689	4688	4687	4691	4693	4694	4670	4671	4673	4675	4647	4656	4655	4654	4649	4650	4665
DEPTH IN METERS	4182	4420	1292	1340	1919	2471	2766	2481	2870	2775	1609	380	567	179	541	1378	665	684	3309	3241	3499	1788	552	799	2760	3974	1862	2738	2852	2358	647	799	2442	1312	631	1331	1073	567	996	1016	1844	1064	366	680	1102	746	1265	859	1587
N LATITUDE	35°22'	34°10'	35°17'	36°01'	36°08'	35°59'	37°15'	38°51'	38°26'	37°26'	38°17'	38°22'	37°12'	36°49'	35°06'	33°52'	32°30'	31°37'	34°58'	37°49'	36°01'	33°44'	32°48'	32°05'	32°33'	35°46'	35°34'	34°24'	34°03'	32°59'	32°06'	32°06'	33°32'	32°42'	31°49'	33°17'	35°08'	36°02'	35°49'	36°16'	35°55'	35°21'	37°09'	37°59'	37°50'	39°04'	39°35'	40°14'	40°15'
LONGITUDE	10°23'W	10°30'↑	07°25'	03°58'	02°21'	00°53'	01°30'E	03°27'↑	05°33'	07°02'	09°31'	11°22'	11°34'	12°54'	15°44'	15°47'	15°49'	17°32'	19°24'	19°19'	21°37'	23°18'	23°13'	25°16'	26°03'	28°28'	29°49'	29°34'	30°12'	30°28'	30°41'	32°05'	32°09'	32°43'	33°29'	34°59'	34°56'	35°03'	23°27'	24°18'	25°16'	26°40'	23°38'	25°31'	26°25'	24°54'	23°53'	24°42'	25°18'
Globigerina bulloides d'Orbigny	38	27	40	51	56	52	29	22	25	31	40	35	23	20	9	11	13	17	17	15	16	10	11	14	16	18	18	10	15	7	14	13	16	11	9	8	14	16	11	17	11	18	18	16	22	22	16	15	18
G. digitata H.B. Brady			.3	.4	.2	.4	.7	1	.2				.3			.8	1	.6	1	2	2	.5	.2			.2	.2		1	.7		.3	.2	.6	.3	.2	.8			.3	.3	.2				.4	.3	.2	
G. eggeri Rhumbler	2	1	3	1	2	.7	.8	3	1	2	5	18	5	2	10	2	2	2	9	10	6	4	3	3	3	6	13	10	6	3	3	5	6	6	6	34	13	19	20	28	22	25	16	22	27	25	3	4	21
G. inflata d'Orbigny	10	8	11	29	28	33	38	28	26	21	14	14	35	31	5	6	3	.4	5				.2		4			1				.3	.2							11		6	2						1
G. pachyderma (Ehrenberg)		.8	.2	.4	.6	.3		.6	.2	.3	1	4	.3		.4	.3	.2	.4	3	.2	.5		.2		1	.2	1	2		.1		.8	.5	.3	.3	4	1	2	2	4	.5	4	.7	2	.8	1	.7	2	2
G quinqueloba Natland				.4		.1					.2	8	1	1	.6	.8			2					.2		1	.4	1			.2	.3		.3		2			.6	1	.5	1	.7			.8	5	2	4
Globigerinella aequilateralis (H B Brady)	1	2	3	1	1	.1	1	2	3	2	2	.2	1	1	5	4	1	2	3	1	4	3	2	.5	7	1	1	2	.6	2	1	.5	.2	1	.5			.3	2	.8	1	1	.4	2	.8	.8	.7	1	1
Globigerinita glutinata (Egger)		4	4	1	.4	.7	2	.2	.7	3	3	2	1	1	.4	1	2	.2	4	1	3	.5	.2	.7	4	.7	1	2	.2			.5	.7		.7	.2	.4	.3	.7	2	1	1		.5	.6	2	4	1	
Globigerinoides conglobata (H B. Brady)	5	1	.2																.1																														
G. rubra (d'Orbigny)	23	24	16	10	9	8	17	25	24	20	23	14	23	35	51	54	55	64	41	64	52	70	70	72	48	68	59	61	60	71	77	69	63	67	68	44	65	59	60	33	59	36	59	52	47	47	69	73	51
G. sacculifera (H.B. Brady)	10	9	9	3	.7	1	.6	2	2	5	.4	.6	2	3	13	11	10	10	4	3	12	10	12	7	14		5	7	11	12		5	10	11	8		3	.1	1		1	.2	3	3		.4	.3		
Globorotalia hirsuta (d'Orbigny) & var.	2	6	3	.4		.1																																											
G. punctulata (d'Orbigny)			.5																																														
G scitula (H.B. Brady)	2	2	2	.3			.1				.2	1				.5			4							.2		.7								8				2		1						.2	
G. truncatulinoides (d'Orbigny)	6	11	5	.4	.6	2	8	11	14	12	8	1	5	4	2	1	1	.2	1	.2								.2												.3		.2	.2						.3
Hastigerina pelagica (d'Orbigny)									.2							.5	.7	.4		.6	.7			.7	1	.7	.4		.3	.3	.2	.3	.5		.5		.8	.3	.6		1								.3
Orbulina universa d'Orbigny	.3	2	3	1	2	1	3	5	4	4	3	2	3	2	3	7	12	2	4	3	5	2	1	2	2	3	1	3	7	4	5	6	2	3	7		1	3	2	1	3	5	.2	2	2	.4	1	1	1
Pulleniatina obliquiloculata (Parker & Jones)	.3	1																																															


BLACK SEA
DARDANELLES
ADRIATIC SEA
TYRRHENIAN SEA
SICILY
CRETE
MONACO
TUNIS
ALGIERS
GIBRALTAR
GAZA
SUEZ CANAL
40°
30°
20°
10°
0°
4694
4693
4691
4687
4688
4689
4686
4685
4683
4681
4678
4698
4676
4675
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4734

Fig. 1. Mediterranean Sea showing locations of stations.

synonymous with, *G. elongata* (d'Orbigny) and *G. helicina* (d'Orbigny), reported by D'ORBIGNY from Rimini, Italy, *G. adriatica* (Fornasini), and *G. rubra* var. *pyramidalis* (vanden Broeck). *G. sacculifera* includes a form listed by various authors as *G. triloba* (Reuss) and described by REUSS from the Miocene of the Vienna Basin. Specimens of *Globigerina eggeri* are small but otherwise typical except for Aegean specimens which frequently have a final whorl consisting of 3½ chambers. The latter are similar to *G. bulloides* and further study may modify the ratios of the two species in Aegean Sea samples. *Hastigerina pelagica*, not reported from the Atlantic in significant numbers, is found in low frequencies chiefly in the eastern Mediterranean.

The relative percentages of the planktonic species are listed in Table I. Included in this table, for comparative purposes, are data for three stations from the Atlantic in the general vicinity of Gibraltar. The data for stations 4637 and 4736 are taken from PHLEGER, PARKER and PEIRSON (1954). The following discussion deals only with occurrences as they appear in this table. Species with frequencies of less than 0·2%, therefore, are not included although they may occur. The sampling is sparse for such a large area but the percentage data show clearly that there are three distinctive populations. The first of these is that of the western Mediterranean which extends east to include station 4721A. This assemblage differs from that of the adjacent mid-latitude Atlantic in the following ways:

	Atlantic (mid-latitude)	*Western Mediterranean*
Globigerina digitata	absent	present
G. inflata	8–13%	14–30% (usually more than 20%)
G. quinqueloba	absent	present
Globigerinoides conglobata	present	absent
G. sacculifera	9–10%	less than 1–5%
Globorotalia hirsuta	present	first 2 stas. east of Gibraltar only
G. punctulata	present	absent
G. scitula	2%	less than 1% (scattered)
Hastigerina pelagica	absent	present (1 sta.)
Pulleniatina obliquiloculata	present	absent

The second assemblage is found in the eastern Mediterranean. It differs from that of the western area in the following ways:

	Western Mediterranean	*Eastern Mediterranean*
Globigerina bulloides	20–56%	8–18%
G. inflata	14–38%	0–6%
Globigerinoides rubra	1–25%	41–77%
G. sacculifera	1–5%	3–14% (except 4 stas.)
Globorotalia truncatulinoides	less than 1–14%	0–2% (scattered)
Hastigerina pelagica	at 1 sta.	consistent occurrence

The third assemblage is found in the Aegean Sea. It differs from that of the eastern Mediterranean in the following ways:

	Eastern Mediterranean	*Aegean Sea*
Globigerina eggeri	2–13% (except 2 stas. off Israel)	3–28% (mostly more than 20%)
G. pachyderma		slight consistent increase
Globigerinoides sacculifera	3–14%	0–3%

In the western Mediterranean the population must be adapted to a wider temperature range than that found in the adjacent Atlantic. The winter temperatures are more nearly analogous to those found on the western Atlantic continental slope in mid-latitudes. In some respects the western Mediterranean population reflects this and shows a resemblance to the populations in that area (PARKER, 1948; PHLEGER, 1939, 1942) as shown by the high frequencies of *Globigerina bulloides* and *G. inflata* and the low frequency of *Globigerinoides sacculifera* as well as in lesser respects. The fauna occurring at the three stations (4732–4734) just east of Gibraltar is of interest. Two of these stations lie within the low temperature area reported by ROUCH (1940). Here exceptionally high frequencies of *Globigerina bulloides* and low frequencies of *Globigerinoides rubra* and *Globorotalia truncatulinoides* are found. Whether or not these changes are due to a lowered mean temperature maximum is a matter of speculation. The presence of *G. hirsuta* in significant frequencies in this area may be due to transport by the entering Atlantic current. The faunas reported by MURAOUR (1954 A, B) from the vicinity of Algiers show a much lower percentage of *Globigerinoides rubra*. The populations reported by PHLEGER (1947) from the Tyrrhenian Sea are analogous to those found in the present study.

The increase in the mean minimum temperature in the eastern area from 13° C to 16° C may account for some or all of the shifts in population found there, as similar trends occur when passing from mid to low latitudes in the Atlantic. In general there is a decrease in such species as *Globigerina bulloides* and *G. inflata*, which occur in high frequencies in mid-latitudes, and an increase in *Globigerinoides sacculifera* which is found in increasingly high frequencies in low latitudes.

In the Aegean Sea the mean minimum temperature is 13° C, as it is in the western Mediterranean, which may account for the more consistent occurrence of *Globigerina pachyderma* and the decrease in *Globigerinoides sacculifera* as compared to eastern area occurrences. Lower salinities in the northern part and/or changes in the chemistry of the surface water resulting from the inflow of water from the Black Sea may also account for these changes. This may be especially true in the case of the high frequencies of *Globigerina eggeri* and the fact that many of the specimens are atypical.

The populations at several stations, besides those noted previously, show unusual features but two are especially noteworthy. Station 4724A contains what appears to be a "colder water" fauna. There are higher frequencies of *Globigerina eggeri*, *G. pachyderma*, and *G. quinqueloba* and lower frequencies of *Globigerinella aequilateralis* and *Globigerinoides rubra*. *Globigerina eggeri* is the only species of the group which does not fit this pattern, since that species is found in higher frequencies in low latitudes. Further study may reveal whether or not this fauna is pre-modern. The sample from station 4718 contains a large percentage of weathered, discoloured specimens, some of which are filled with glauconite. This suggests that little deposition has taken place in this area for a long time, since at most stations the planktonic specimens appear to be fresh and well-preserved, showing recent deposition. It is possible that there is a strong current in this area which removes the specimens as they are deposited, leaving the older, filled tests.

The planktonic populations in the Mediterranean probably are derived in two ways: from material brought in by the Atlantic current and from ancestral stock indigenous to the area, a so-called " relict " fauna. A third possible source may be transport through the Suez Canal, but too little is known about this at the present time to evaluate its importance. A study of Table I and of the specimens themselves leads to some interesting speculations on this point. Phleger (1947) believes that occasional specimens of *Globorotalia scitula* are introduced from the Atlantic, but that the species is not found living here. The present findings point to the same source, but it is probable that there is some survival as there is a scattered occurrence of the species throughout the area. *Globigerinoides conglobata* and *Globorotalia hirsuta*, which occur rarely at many stations, may have a similar origin. On the other hand *Globigerina digitata* and *Hastigerina pelagica*, which are rare in modern Atlantic sediments, may be species indigenous to the Mediterranean. The atypical form of *Globigerina eggeri* found in the Aegean Sea is probably an indigenous form.

A recent study of the coiling direction of *Globorotalia truncatulinoides* by Ericson, Wollin and Wollin (1954), shows that the North Atlantic may be divided into provinces in which there occur " races " showing a dominance of left or right coiling. According to their interpretation the area immediately west of Gibraltar should contain a population showing equi-directional coiling. Samples from *Atlantis* stations 4637, 4735 and 4736 were examined and this was found to be the case. East of Gibraltar at station 4734 the ratio shifts to 79% left coiling (based on 62 specimens) and increases rapidly to the east until at station 4730, just east of 0° Long., a dominance of 99% left coiling is found. High ratios of 88% or more are maintained eastward to station 4711, just west of 20° E. Long., which shows 62% left coiling. Farther east there are too few individuals to give significant results. Where possible, 400 specimens were counted and such samples served to check neighbouring stations containing fewer specimens. These results also suggest that at least part of the Mediterranean populations are indigenous and not directly derived from the Atlantic. A study of other species by statistical analysis of measurements or other characteristics and a comparison with Atlantic specimens would give additional data on this point.

REFERENCES

Di Napoli-Alliata, E. (1952), Foraminiferi pelagici e facies in Italia. *Atti VII Conv. Naz. Met. e Petr., Taormina*, 1952, 1–34.

Ericson, D. B., Wollin, G. and Wollin, J. (1954), Coiling direction of *Globorotalia truncatulinoides* in deep-sea cores. *Deep-sea Res.*, **2**, 152–158.

Kruger, D. (1950), Variations quantitatives des protistes marins au voisinage du Port d'Alger durant hiver 1949–1950. *Bull. Inst. Océan., Monaco*, 978, 1–20.

Muraour, P. (1954 a), Sur quelques sédiments dragués au large du littoral compris entre le Cap Djinet et l'embouchure de l'Oued Sebaou. *Recherches sur les Fonds Chalutables de la Région d'Alger. Com. Loc. Océan. Études Côtes Algérie*, 91–107.

Muraour, P. (1954 b), Étude d'une vase prélevée à 700 mètres de profondeur, au large de la Baie de Castiglione. *Recherches sur les Fonds Chalutables de la Région d'Alger. Com. Loc. Océan. Études Côtes Algérie*, 123–132.

Oren, O. H. (1952), Some hydrographic features observed off the coast of Israel. *Bull. Inst. Océan., Monaco*, 1017, 1–9.

PARKER, F. L. (1948), Foraminifera of the continental shelf from the Gulf of Maine to Maryland. *Bull. Mus. Comp. Zool.*, **100** (2), 213–241.

PHLEGER, F. B (1939), Foraminifera of submarine cores from the continental slope. *Bull. Geol. Soc. America*, **50**, 1395–1422.

PHLEGER, F. B (1942), Foraminifera of submarine cores from the continental slope. Pt. 2, *Bull. Geol. Soc. America*, **53**, 1073–1098.

PHLEGER, F. B (1947), Foraminifera of three submarine cores from the Tyrrhenian Sea. *Göteborgs Kungl. Vetensk. och. Vitterhets-Samhälles, Handl.*, Sjätte Följden, Ser. B, No. 5, 1–19.

PHLEGER, F. B, PARKER, F. L. and PEIRSON, J. F. (1953), North Atlantic core Foraminifera. *Repts. Swedish Deep-Sea Exped.*, **7**, 1–122.

POLLAK, M. (1951), The sources of the deep water of the eastern Mediterranean Sea. *Jour. Mar. Res.*, **10** (1), 128–152.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 212-223.

Hypotheses connecting fluctuations in Arctic climate with biological productivity of the English Channel

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Summary—An explanation of variations in nutrient content and biological productivity in the English Channel in the last thirty-five years has been sought in terms of variations in Arctic climate. To provide the connecting links a series of interlocking hypotheses has been erected. These are summarized in the discussion.

For many years at Plymouth we have been concerned with the large variations in the phosphorus available for growth of plants and animals as represented by the amount of phosphate present at the midwinter maximum (Fig. 1). This was high during the nineteen-twenties, fell to a little more than half during the nineteen-thirties and forties, and is now tending to increase again. There have been large associated changes in the abundance and nature of the zooplankton in the English Channel.

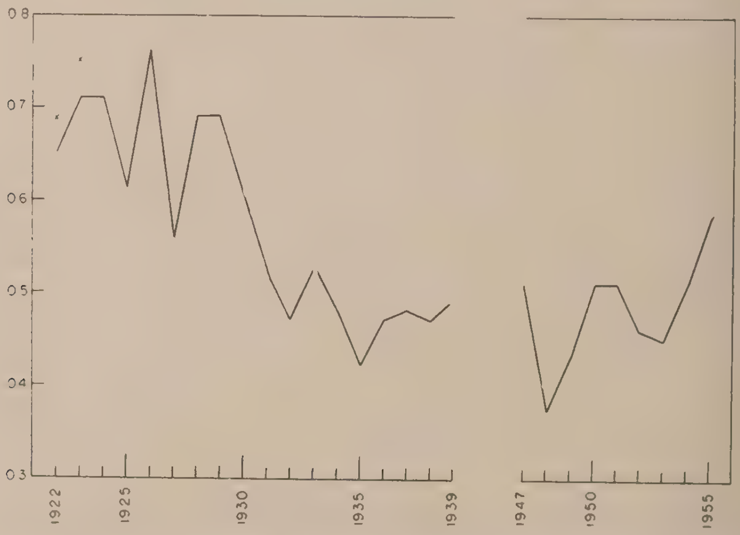

Fig. 1. Annual variations in inorganic phosphate available for plant growth at a position in the English Channel, 22 miles south-west of Plymouth, as measured at the winter maxima. In 1922 and 1923 the maxima were probably missed; they were probably greater than shown.

For some years we sought an understanding from studies on the continental shelf within 200 miles of Plymouth (the Celtic Sea) and found none. The next step was to examine the conditions over the continental slope of the Celtic Sea (Cooper, 1952 b). Upwelling on the scale which occurs along the coasts of California, Peru and South-west Africa has never been recognized, since the prevailing winds are unfavourable for this. Even when winds have been favourable for upwelling of nutrients by the classical process, as in February, 1947, this has not occurred.

The phenomenon of cascading was first examined (Cooper and Vaux, 1949) and is now well authenticated (Lee, 1952; Boden and Kampa, 1953). It is primarily a process of impoverishment, stripping from the shelf whatever nutrients happen to be there. Work now in progress (1955) shows that this concept is too simple, and that there may be an associated mechanism which leads to enrichment of water overlying a cascade, though not of the area from which the cascade has come.

Other hypothetical processes of enrichment, such as capsizing and submarine eagres (Cooper, 1952 a, d) have also been proposed, but still lack observational basis.

At this point in the investigation, a satisfactory explanation of the fluctuations in phosphate and biological productivity was still not in sight. There was no escaping the conclusion that an answer would never be found whilst study was confined to the shallow shelf.

Then an investigation was undertaken which seemed at the time to be a false scent, viz. the search for an explanation of the sudden appearance off Plymouth in the autumn of 1950 of large numbers of boar fish, *Capros aper*. The hypothesis was erected that these had been ejected about six weeks earlier from their normal habitat in a coral-encrusted submarine canyon by a submarine eagre. A rider necessarily followed, that the conditions in the Atlantic abreast of the slope between depths of 200 and 500 m must have been very different in the nineteen-thirties and forties from what it had been in the nineteen-twenties. The *Capros* argument (Cooper, 1952 c) was a logical one, but the threads were as thin as gossamer. It may well prove utterly wrong. None the less it was this study which led to the decision that it was useless further to pursue studies in shallow water, but that the deeper Atlantic ocean must hold the key.

There is no need to invoke hypothesis to establish that—whatever the mechanisms may be—vertical mixing down to about 400 m occurs in winter south-west and west of the English Channel. The conclusion is evident from every station that has ever been worked there. There seems no good reason for believing that there has been any major change in the nature of the physical processes occurring in the upper 400 m during the last 40 years. However, the chemistry of these waters has changed, and we are forced to seek an explanation in terms of physical processes occurring at a greater depth. The enrichment with nutrients of the upper 400 metres can have come about only by some form of overall upward displacement of the deeper water. The idea is that, first, during the rich period, the layer of water containing, say, 0·8 to 0·9 μg–atom l phosphate-P had been displaced upwards by some hundreds of metres, so that the processes of vertical mixing always operative in the upper 400 metres can bring them right to the surface, and that, secondly, during the poor years from 1931 to about 1950, this layer had subsided so that the mixing processes could no longer bite into it. Nutrient evidence to establish this argument beyond doubt does not exist. Due to internal waves, the observed depth of a nutrient sample obtained by snap sampling may differ by scores of metres from the mean depth. Consequently the sparse data available from earlier years are hard to interpret. Argument can proceed only *ex hypothesi*.

To achieve such a large-scale upward displacement of water, an equivalent volume at a greater depth, perhaps at the very bottom of the Atlantic, had to arrive from somewhere else. Such deep water is always cold and has sunk from the surface in polar regions.

Two events are necessary for the production of deep, bottom water in polar regions: one is that there must be present water of sufficiently high salinity, the other is that air temperatures must be low enough to cool this saline water sufficiently for it to become very heavy and so able to sink deep in the ocean.

Deacon (1937) has shown that this happens in the Weddell Sea and around the South Orkney Islands. Taking the world as a whole, this part of the Antarctic is by far the most important centre for creation of oceanic bottom water. As this water moves away from the Antarctic it may become much modified by mixing processes, particularly over the deep submarine ridges which separate the deep oceanic basins.

In the North Atlantic there are two areas of sinking of cold saline water. One is over the ridge which joins Faeroe to Iceland (Cooper, 1955) and the other is in the Denmark Strait and around East Greenland. In neither case can it be said with strict truth that the cold, heavy water which sinks deep in the Atlantic is formed in a localized area. Rather are we concerned with a continuous process which takes place all the way from Jan Mayen to the Southern tip of Greenland. It so happens, however, that events which happen between 300 metres depth and the sill of the two ridges connecting Iceland with Faeroe and Greenland stand out in high relief.

In the development for the Faeroe–Iceland area (Cooper, 1955) it was suggested that the density distribution associated with the Iceland–Faeroe current acts as a dynamic dam, parting the waters of the Atlantic from those of the Norwegian Sea. Whilst it runs steadily, little water need flow over the ridge. Our increasing knowledge of such currents (cf. Fuglister and Worthington, 1951) suggests that they rarely run steadily for very long and tend to meander all over the place. A meander to the south will carry cold Norwegian Sea water to the Atlantic, where it will lie above much lighter water through which it must sink. Again, if the current weakens, the isopycnals will flatten out. Saline surface Atlantic water will flow into the Norwegian Sea, and in compensation Norwegian Sea water below about 250 m will spill over into the Atlantic. In the neighbourhood of 62° N, 13° W, this cascading water sometimes has a salinity exceeding 35·0‰ and a temperature of less than 2° C. It is responsible for the salinity maximum which can be followed south-west for many hundreds of miles along the Reykjanes Ridge (Cooper, 1955) and round into the Western Basin.

A similar process in the Denmark Strait may differ in detail. The cold but brackish East Greenland current flows south along the coast, whereas the warm saline Irminger current flows from the south of Iceland round by the west to the north coast of Iceland. These two currents throw off spurs which coalesce with their opposite numbers, but in the centre there is a region where the two main currents must be moving more or less side by side and in opposite directions. This is an unstable situation, and must lead to a lot of eddying, swinging about of the main water masses, and mixing. The sill depth of the Denmark Strait is rather more than 500 m. At depths shallower than this north of the Strait there is much water heavier than 27·9 or 28·0 sigma-t and able, if it can escape, to sink into the Atlantic. It comes through the strait banked against the west side. South of the sill it does not fall straight into the trough, but is held against the terrace at depths less than 600 m. It travels south banked against the continental slope of Greenland, and does not reach the bottom until 60° N Lat. The evidence for these statements is being marshalled and will shortly be published. A great debt is due to the workers on the research ships, *Meteor*, *General Greene*, *Dana* and *Heimland*. Full acknowledgements will be made later.

On all sections this piling up of heavy water to the right against the slope is to be seen, but there is much variation in temperature; in some sections there is an abundance of water having potential temperature less than 2° and salinity near to $34{\cdot}91\,^{\circ}/_{oo}$ In others there is no water colder than 2·5°, or, in one " Meteor " section, colder than 3°. There is always a deep current towards the south-west, but the presence of very cold Denmark Strait water is intermittent.

Such intermittent bursting of the dynamic dam, due to either process, would result not in a continuous stream of water flowing off the ridge, but in a series of self-contained, cold, heavy balls or boluses of water. The calving of a large bolus of water from the ridge is likely to be completed in a matter of days or weeks at most, and is likely to occur most often in late winter or early spring. The descent of a bolus from 400–500 to 1,500–2,000 metres through much lighter water is likely to need a very short time. It is not surprising, therefore, that no research ship has ever recognized the birth process for what it may be.

This water does not sink by the shortest route to the bottom of the Atlantic, but is held to the right by the force of the earth's rotation, and so traverses the side of the continental slope for 300 miles to Cape Farewell, and continues in this way around the bottom of the Labrador Sea at least as far as Newfoundland.

The evidence I have presented gives no idea of the frequency with which these cold water masses or boluses are born or calved in the Denmark Strait. It could be a seasonal event, once a year. It seems more likely that the complex water movements there are constantly meandering, and that the thrust of a cold bolus to the south over the sill may be a rather irregular affair. If so, the sinking of boluses along the Greenland coast may also be an irregular affair.

It is helpful to think of one of these boluses as behaving like a solid but elastic object. As it thrusts forward and downward, it must displace the water already there.

Moreover, when passing over an irregular slope and bottom, the under surface of such a bolus of water must be expected constantly to adjust and re-adjust itself to the solid topography. Its free surface against the enveloping water must needs also constantly re-adjust itself. The picture one has is of a vigorously writhing interface which should initiate internal waves in the adjacent ocean, even if this is only weakly stratified.

Shortly after calving, whilst it is sinking rapidly from sill level at about 500 m to 1,500 m, the internal wave pattern should be intense but short lived. After a depth of 2,500 m has been reached, a number of such boluses are likely to be present and in some degree to have coalesced. The writhing will be gentler but unceasing. This writhing of boluses in the North Atlantic provides an origin for internal waves down to at least 4,000 m. In the North Pacific no such possible origin for internal waves has been recognized deeper than the bottom of the sub-Arctic water around 1,500 m. Deeper waves might however arrive in the North Pacific from the Antarctic.

It is commonly believed that the attenuation of such waves in the open ocean is not severe. They may travel great distances. If there is no frictional loss on passage, for a few hundred miles, the energy in a wave propagated in an equipotential surface from a point source will be inversely proportional to the distance run. For greater distances such waves, not accompanied by transport of water, should follow great circles, so that the law of attenuation would need to be worked out not from plane but from spherical trigonometry. However, in the Eastern North Atlantic the source of internal waves is postulated not as a point but as ridges or lines more than 600 miles long. Consequently the energy in waves from these lengthy sources arriving at the European continental slope may be considerable.

Let us now consider what may happen when such a wave system meets a continental slope. If it approaches head on at a smooth gentle slope, it is likely to run straight up it and to be reflected back. A standing wave might well develop off slope, but the conditions are unlikely to lead to a lot of mixing. From the usual snap oceanographical observations such a standing wave might be interpreted as evidence for a strong along-slope current. If the wave system approaches a smooth slope at a wide angle, the waves may swirl along it, and somewhat more mixing would result.

The really interesting case is when an internal wave system approaches a highly dissected continental slope or borderland at a glancing angle. The slope abreast of the English Channel is likely to provide an excellent site for this process, while the Southern Californian continental borderland may provide an even better one. Then, as I see it, there should be a very great deal of sloshing about indeed, much vertical mixing and a tendency for homogenization of all properties as far down as the internal waves occur. This means that nutrients will be brought up to such depths that the classical methods of wind-driven upwelling can bite into the enriched water and bring it right up to the surface. If, and when, cold Arctic winters produce large boluses and consequent internal waves of large amplitude, then upper-water enrichment with nutrients over continental slopes would be favoured.

Furthermore, we may be concerned not only with the conventional nutrients, but with associated organic growth accessory factors which we only dimly understand. Much dead plankton, faeces and organic detritus sink in the sea and decompose. This should happen to the greatest extent in the oxygen poor layer. Oxygen defect (saturation value less content of oxygen observed) provides a very rough but ready measure of the extent of decomposition products. During periods of minimum internal wave activity the maximum oxygen defect may well be more than in periods of great activity. But paradoxically, the depth range of the oxygen poor layer should be less. The inflexion should be more pointed. This is because the homogenizing action of internal waves beating against a dissected slope should spread the oxygen defect both above and below the point of inflexion. The upward spread would bring not only the oxygen defect but also the accompanying organic substances nearer the surface.

In this group of interlocking hypotheses, some may be rejected without gravely imperilling the rest. The concept of homogenization is not one of these for, if it falls, the others become useless. To illustrate the argument, let us assume that some property such as phosphate content is linearly proportional to depth, and is subject to a uniform process of homogenization from surface to an inert bottom. In mid water, exchanges of phosphate will occur, but the later state will remain analytically indistinguishable from the earlier. If a layer was labelled with radiophosphorus, homogenization would spread this up and down so that the result might be seen as a form of eddy diffusion. At the surface, exchange with the air being impossible, a homogeneous layer enriched from below would begin to build up. As the process proceeds, both depth and phosphate content of the homogeneous layer would increase. Similarly at the bottom, homogenization will increase the thickness of a uniform bottom layer containing phosphate equal to that at the point of inflexion. The defect in phosphate content which would seem to have appeared near the bottom has actually been moved upwards, and equivalent enrichment has appeared near the surface. It should be clear that the molecules of phosphate which appear in the surface waters are not those which have left the bottom. The process is akin to water moving up a pipe. If the process went on long enough and unhindered, the whole ocean would become homogenized from top to bottom. At an intermediate stage, it might seem that phosphate was being transported from the bottom to the surface waters, without the middle layers being affected in any way that could be recognized by chemical analysis.

Homogenization is a two-way process. In an ocean in which a nutrient salt increases downwards, the shallower and poorer waters are enriched at the expense of the deeper. Temperature or heat content, on the contrary, decreases downwards so that the same process causes the deeper layers to warm up at the expense of the shallower. Now let us consider an area of the sea near a continental slope: (a) where the broad pattern of currents and winds as well as the amount of radiant energy received from the sun remain unchanged but (b) where the intensity of deeper internal waves derived from distant sources increases. Homogenization should increase so that the surface layers would become colder but richer in nutrients. If then for some years the process is reversed, internal waves from a distance would become weaker so that homogenization against slopes would decrease. Loss of nutrients and accessory growth factors from surface waters by sinking of faeces and detritus would not be fully made good. In consequence the surface waters become poorer. At the same time, radiation received from the sun would be retained in the upper waters, instead of being homogenized by mixing with deeper colder water. The sea surface would warm up. Something very like this seems to have happened in Western European waters in the last thirty years.

The changes in heat balance would be expected to produce some local changes in winds, weather and currents, so that in places this generalization may not apply. Averaged over a large ocean, however, and granted the premises, it seems inevitable.

Again, when very cold winters prevail in the Arctic, more cold heavy water will be produced, and will spill over the ridges between Greenland and the Faeroes into the Atlantic. The scale of everything will be increased, so that the amplitude of the system of deep internal waves in the ocean should also increase.

Let us now consider two oceans. In one, writhing boluses of newly arrived water may initiate internal waves and subsequent homogenization right to the bottom in 4,000–5,000 m. In such an ocean, combination of the two separate processes of upward displacement and homogenization will cause deep capital reserves of nutrients to be made relatively quickly available for biological production in illuminated waters. In the second ocean, sinking of cold water does not go deeper than, say, 1,500 m depth. Below this depth there can be no writhing surfaces, no appreciable internal waves and no homogenization against continental slopes. There is then no way by means of which nutrients below this depth can be got into circulation. Vast resources of nutrient capital remain unused for long periods. In such an ocean only the resources above, say, 1,500 m would be in effective circulation.

In this parable the oceans in mind are the North Atlantic and the North Pacific. The North Pacific is much the larger, so that for it the ratio of length of slope to volume of water is much less than for the North Atlantic. This also militates against the efficient use of the capital resources of the North Pacific by a process of homogenization.

The North Atlantic seems on the whole to be subject to impoverishment by exchange across the equator. Loss of relatively rich deep water, tends to be compensated by inflow from the south of relatively poor surface water. This is a process similar in nature to the impoverishment of the Mediterranean by exchange of waters in the Straits of Gibraltar. Consequently the deep phosphate resources of the North Atlantic are only about one-third of those of the North Pacific. In spite of this, the North Atlantic contains many of the world's richest fisheries. It is true that the North Atlantic contains an undue proportion of the shallow shelves well suited to the growth of fish, and that it is bordered by enterprising communities who make the most of what nature offers. But when all allowance is made for these important considerations, it still seems that the biological productivity of North Atlantic waters is greater than it ought to be. The nutrient capital of the North Atlantic seems to be more efficiently used than that of the North Pacific, except around Japan. The interlocking hypotheses offered here provide a possible explanation of this.

Again, judged by its phosphate resources the Mediterranean should be a near-desert sea. Though not rich, it is certainly not a biological desert. Here again one is forced to the conclusion that the slender phosphate capital of the Mediterranean is put to maximum use. It might be worth enquiring whether the present hypotheses could be usefully applied there.

Attention has been focussed on the events possibly initiated by calving of boluses of heavy cold water over ridges in high latitudes. There is another and different mechanism which may produce similar results on a smaller and shallower but not negligible scale. It may be illustrated from the Straits of Gibraltar. Here, light Atlantic surface water flows into the Mediterranean, and heavy, relatively cold and very saline deeper Mediterranean water flows out. In nature it is becoming ever more evident that fluid motions such as this tend to be irregular or gusty. It is reasonable to suppose that the outflow of Mediterranean water may not be as a steady stream, but as a series of boluses separately calved. This would initiate a chain of events similar to those already described for Faeroe–Iceland water, and augment the efficient use of the nutrient capital of the Atlantic. It is less easy to see how this calving process into the Atlantic might influence the Mediterranean regime, but some effect there is possible.

Two distinct speculative mechanisms have been described to transfer energy through deep water from one part of an ocean to another and, by so doing, to facilitate enrichment of surface waters with nutrients. These are (1) the hypothesis of upward displacement due to the intrusion of colder and heavier waters at a greater depth, and (2) the hypothesis of transfer of energy by internal waves, initiated by the sinking of boluses of cold, heavy water calved from ridges in high latitudes. These two hypotheses need not be mutually exclusive, but may merely express facets of a complex system of energy transfer at depth. This, in the words of OTTO PETTERSSON, might be described as the systole and diastole of the ocean. Only many observations well placed in space and time may show what weight should be given to each or any of the component hypotheses.

Finally, the whole argument suffers from a grave thermodynamic weakness. Thermodynamically, energy can be obtained only from a source and never from a sink.

The areas around the Faeroe–Iceland Ridge and the Denmark Strait are sinks in every sense of the word. Consequently, not until the argument is geared to a thermodynamic source can it be fully satisfactory.

A chain of hypotheses has been constructed to link fluctuations in Arctic climate with fluctuation in the biological productivity of the English Channel. The author is under no illusions as to their vulnerability to attack from many directions. He can hope only that, by offering a target, something more substantial may emerge.

There is climatic evidence in support of the hypotheses.

Smed (1947, *et seq.*) has collected and summarized all the records of surface temperature which have been collected in the North Atlantic. Fig. 2 shows the areas into which he has divided the North Atlantic. His areas B, C, D are those in which we are most interested. A series of cold winters was experienced in the 'teens of this century, and particularly in 1918, 1920 and 1921. In the same Figure the departures from the long term average of the sea temperatures in April, 1920, and April, 1921, are presented. These were the culmination of a series of cold winters when a great amount of North Atlantic bottom water must have been formed.

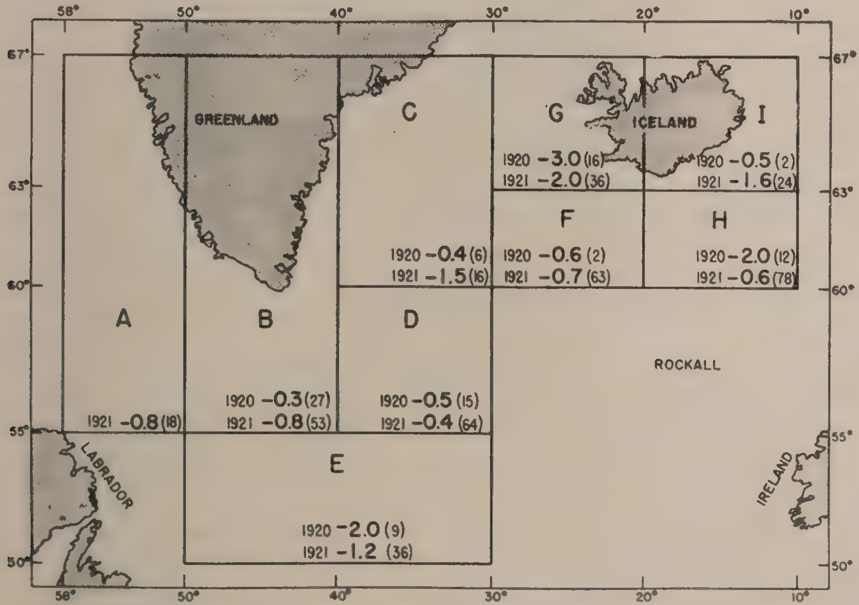
58°
50°
40°
30°
20°
10°
67°
63°
60°
55°
50°
GREENLAND
ICELAND
LABRADOR
IRELAND
ROCKALL
A
1921 −0.8 (18)
B
1920 −0.3 (27)
1921 −0.8 (53)
C
1920 −0.4 (6)
1921 −1.5 (16)
D
1920 −0.5 (15)
1921 −0.4 (64)
E
1920 −2.0 (9)
1921 −1.2 (36)
F
1920 −0.6 (2)
1921 −0.7 (63)
G
1920 −3.0 (16)
1921 −2.0 (36)
H
1920 −2.0 (12)
1921 −0.6 (78)
I
1920 −0.5 (2)
1921 −1.6 (24)

Fig. 2. Northern North Atlantic. Average departures of sea surface temperatures (°C) from long term means in the months of April 1920 and 1921. The number of available observations averaged is shown in brackets (after Smed).

Air temperatures between 60° and 70° N have been recently summarized by Brown (1953). Fig. 3 shows the area studied divided in Marsden squares. Unfortunately, for squares 220 and 221 (in which we are most interested) there are insufficient data for evaluating means. His decadal means for areas 217A and B and 218A and B are shown in Fig. 4. It will be seen that the decade 1910–1919 in December–March was

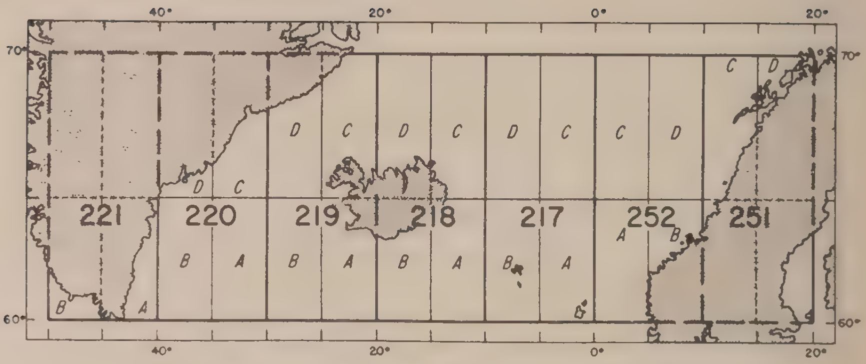

Fig. 3. Chart showing position of Marsden squares 217 and 218.

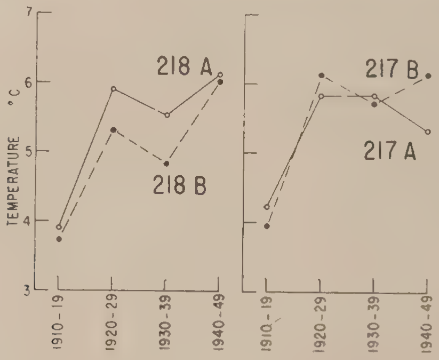

Fig. 4. Decadal mean air temperatures for Marsden square areas 217A and B and 218A and B for the season December to March (after P. R. BROWN).

$1\frac{1}{2}$° colder than the three decades 1920–49. That is on a decadal basis the years 1910–19 were more suitable for the formation of oceanic bottom water than the thirty years since. It is probable that in these decadal means the coldness of the years 1920 and 1921 was swamped by the eight following warm years. Nothing comparable was experienced for the next thirty years. In these years we had precisely the conditions which we need to explain the fluctuations in the English Channel. In each winter an amount greater than average sank in the Greenland area. In the first winter the excess sinking would have displaced the strata of water upwards by, perhaps, a few tens of metres. This would not have brought much nutrient rich water within reach of the processes of vertical mixing of surface waters which are always operative. The next winter would have been more effective and the third winter most effective of all. By this time the nutrient table would have been lifted by perhaps 100 metres or more, to a level at which processes of vertical mixing would readily and continually draw upon the upwardly displaced water to enrich the surface waters. The deep waters of the ocean move slowly, so that there may be a considerable time lag before events in polar regions come to influence upward displacement in temperate and tropic latitudes.

On this line of argument, the maximum enrichment of the surface waters of the temperate Eastern North Atlantic with nutrients occurred in or shortly after the year 1921.

If unusually large amounts of water sank in the North in these winters, they had to be compensated by an equivalent amount of surface water, which could have been supplied only by increased intensity of the North Atlantic Drift system. One event associated with this increase in the North Atlantic Drift may be the incursion into the English Channel of much unseasonably warm water in the autumn of 1921 (Harvey, 1925).

We have long had the suspicion that this incursion of warm water was in some way associated with the rich phosphate observed by Atkins in his first analyses in the English Channel on 7 March, 1923. I, for one, have always had great difficulty in accepting this explanation, since warm surface water is nearly always poor in nutrients. Today there is no such warm water anywhere in the Bay of Biscay or Eastern North Atlantic carrying an equivalent supply of nutrients. This objection now vanishes.

This water in some area well to the south of the British Isles had been enriched with nutrients by upward displacement following a period of cold Arctic winters and the three winters of excessive polar sinking. During the warm summer of 1921 there was time for the water to warm up by solar heating, but no considerable redistribution of nutrients with the deeper water had taken place. The nutrient properties of this particular warm water may well have been very far from the equilibrium state that we commonly observe.

DISCUSSION

During the last thirty-five years there have been large changes in the distribution of phosphate in the Western English Channel whilst the zooplankton has changed in species and abundance. No explanation has been found locally, so that attention has been extended to events in the Atlantic Ocean.

A number of associated hypotheses have been erected to explain these changes in the English Channel:

(1) That in cold Arctic winters saline surface water is cooled further and made heavier than in relatively mild ones.

(2) That this leads to a greater recruitment of fresh deep water in the North Atlantic after cold Arctic winters.

(3) That to make room for this fresh deep water, an equal volume of water has to be displaced upwards, i.e. a supply of nutrient-rich deep water is displaced towards the illuminated surface layers. This process may be a diffuse one over the whole ocean basin.

(4) That the origin of the North Atlantic deep water should be considered not in terms of a localized area, but in terms of physical processes which are occurring all the way from Jan Mayen (72° N) to the southern tip of Greenland (58° N), and even further south.

(5) That in so far as special areas stand out, these lie over the ridges between Iceland and Greenland on the west, and the Faeroe Islands on the East. Over the two ridges the physical processes which yield heavy water seem to differ in detail, but in both are

confined to depths between about 300 m and the sill depth of about 550 m. Local surface waters seem not to be overmuch concerned.

(6) That the cold heavy water flows away from the sills of the two ridges not as a smooth continuous current, but intermittently as discrete large boluses.

(7) That due to the effect of the earth's rotation these boluses are held strongly to the right against the eastern slope of the Reykjanes Ridge, and against the eastern continental (or insular) slope of Greenland.

(8) That where the boluses are constrained by restricted topography, they move fast horizontally and sink slowly.

(9) That where narrow straits open out to oceanic dimensions and constraints are removed, then horizontal velocity decreases and the boluses sink rapidly.

(10) That where boluses of heavy water pass over a dissected bottom or slope, they mould themselves to the rock configuration, and that in consequence the free interface against the enveloping water writhes vigorously.

(11) That such a writhing interface, at what is effectively a strongly developed discontinuity layer, initiates strongly developed internal waves which may travel great distances through the open ocean with little attenuation.

(12) That when such waves meet a continental slope vertical mixing should result, and that when they meet a highly dissected continental slope at a glancing angle, the mixing should be very vigorous indeed. Homogenization of all properties would be much favoured, i.e. shallower layers would be enriched with nutrients at the expense of the deeper and, conversely, deeper layers would, in most places, be warmed at the expense of the shallower.

(13) That the nutrients are finally brought to the surface by thermal and wind-driven mixing processes, and by upwelling processes which may be always operative. It is suggested that these processes are much more effective in producing surface enrichment when a series of cold Arctic winters has produced a situation in the deep Atlantic which favours upward displacement and homogenization of nutrients, especially against continental slopes.

(14) That in the North Pacific there is no exact parallel to events in the North Atlantic. The only comparable process would seem to be unable to affect the North Pacific waters deeper than about 2,000 m at most. Consequently the nutrient resources of the deep North Pacific seem to be much less effectively used than are those of the deep North Atlantic.

Some evidence for hypotheses 1–9 has been presented elsewhere (COOPER, 1955). Further evidence for hypotheses 1–9, applying to the Denmark Strait and East Greenland, is being marshalled for publication.

Hypotheses 10 and 11 are intuitive and no supporting evidence is known to the writer.

Direct observations in support of hypotheses 12 and 13 are now being sought in the Atlantic near Plymouth. Further evidence in support of hypothesis 14 is still being sought.

REFERENCES

BODEN, B. P. and KAMPA, E. M. (1953), Winter cascading from an oceanic island and its biological implications. *Nature*, **171**, 426–427.

BROWN, P. R. (1953), Climatic fluctuation in the Greenland and Norwegian Seas. *Quart. J. Roy. Met. Soc.*, **79**, 272–281.

COOPER, L. H. N. (1952 A), Processes of enrichment of surface water with nutrients due to strong winds blowing on to a continental slope. *J. Mar. Biol. Assoc., U.K.*, **30**, 453–464.

COOPER, L. H. N. (1952 B), The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *J. Mar. Biol. Assoc., U.K.*, **30**, 465–526.

COOPER, L. H. N. (1952 C), The boar fish *Capros aper* (L.), as a possible biological indicator of water movement. *J. Mar. Biol. Assoc., U.K.*, **31**, 351–362.

COOPER, L. H. N. (1952 D), Water movements over the continental slope in relation to fisheries hydrography. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **131**, 44–50.

COOPER, L. H. N. (1955), Deep water movements in the North Atlantic as a link between climatic changes around Iceland and the biological productivity of the English Channel and Celtic Sea. *J. Mar. Res.* (in press).

COOPER, L. H. N. and VAUX, D. (1949), Cascading over the continental slope of water from the Celtic Sea. *J. Mar. Biol. Assoc., U.K.*, **28**, 719–750.

DEACON, G. E. R. (1937), The hydrography of the Southern Ocean. *Discovery Repts.*, **15**, 1–124.

FUGLISTER, F. C. and WORTHINGTON, L. V. (1951), Some results of a multiple ship survey of the Gulf Stream. *Tellus*, **3**, 1–14.

HARVEY, H. W. (1925), Hydrography of the English Channel. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **37**, 59–89.

LEE, A. J. (1952), The influence of hydrography on the Bear Island cod fishery. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **131**, 74–102.

SMED, J. (1947 *et seq.*), Monthly anomalies of the surface temperature in the sea round South Greenland during the years 1876–1939. *Ann. Biol., Cons. Perm. Int. Expl. Mer*, **2**, 16–22. (See also, 3, 12–24; **4**, 11–26, 57–60; **5**, 11–15; **6**, 18–27; **7**, 9–13, 85–88; **8**, 20–22; **9**, 16–21, 95.)

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Review of the oceanography of Long Island Sound

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Summary—Long Island Sound is a shallow, semi-enclosed body of slightly brackish (23–31 ‰) water with an area of about 900 nautical square miles. Moderate tidal currents permit a small seasonal thermocline and slight vertical gradients in salinity, oxygen and nutrient salts. The major feature of non-tidal circulation is a two-layered transport system in which a freshened surface layer moves eastward out of the Sound and is replaced by a more saline inflow along the bottom. The latter contains more nutrients than the outflowing surface water, so that the transport system tends to accumulate and conserve nutrients. Freshwater drainage also makes a significant contribution of nitrate.

Phytoplankton concentrations are large, but the species composition is relatively limited. A large diatom flowering occurs in late winter, following an early winter minimum, with only minor fluctuations the rest of the year. There is sufficient mixing to prevent a large accumulation of nutrients in the bottom water, so that there is neither pronounced poverty in summer nor a big autumn flowering following destruction of the thermocline. Major limiting factors are the amount of effective light in autumn and winter and the nitrogen supply in spring and summer. Variations in light and temperature from one year to the next affect the winter species composition and the time of the flowering. Diatoms are largely replaced in summer by naked flagellates and other nannoplankton. During one summer when nitrate concentrations were higher than usual, diatoms were abundant and there was also an unusually large zooplankton crop. A causal connection is indicated but not well established.

The zooplankton consists of large numbers of small animals. Relatively few species are present. The dominants are two species of the copepod *Acartia* which alternate seasonally. Descriptive and experimental studies suggest that seasonal replacement is primarily a temperature-controlled competition rather than a direct, lethal temperature effect. Experiments show that the *Acartias* have high respiratory rates and low grazing rates compared with most other copepods that have been examined and possibly are able to achieve dominance only in waters sufficiently brackish to exclude more efficient oceanic species.

Preliminary studies of bottom fauna indicate a relatively large biomass, again consisting of large numbers of small animals. Fish eggs and larvae are abundant, and the Sound may be an important spawning and nursery ground. However, commercial fishery statistics show no indications of a large population of mature fish.

Total phytoplankton production is about the same as in the open coastal and bank waters off New England. Most of this production is utilized in the support of small animals which do not provide an adequate food supply for the efficient production of large carnivores.

INTRODUCTION

LONG ISLAND SOUND, like other New England waters, has been a source of interest and livelihood since colonial times, and its general features are well described in early expedition narratives. Scientific studies of its waters began a little more than a hundred years ago with a survey of the morphometry, character of the bottom, tides, and currents, jointly sponsored by the Navy and the predecessor of the present Coast and Geodetic Survey. The pertinent information was printed on a series of three excellent hydrographic charts in 1855. More thorough surveys of tides and currents were made during the late nineteenth and early twentieth centuries, and all available observations have been summarized by LE LACHEUR and SAMMONS (1932).

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The first oceanographic studies that may be regarded as modern in their general scope and outlook were begun in the 1870's under the able direction of SPENCER F. BAIRD, U.S. Commissioner of Fish and Fisheries. For the waters from Cape Cod to New Jersey, and including Long Island Sound, we find in his reports during the ensuing years not only accounts of the fishes and their physical environment, but also monographs on the invertebrates (VERRILL, 1873) and algae (FARLOW, 1879), as well as other major works that are still in common use.

In 1935 the U.S. Fish and Wildlife Service established a laboratory at Milford, Connecticut, under the directorship of VICTOR L. LOOSANOFF. One of the most important contributions of this laboratory has been a thorough study of lamellibranch physiology and ecology by combined field and laboratory techniques. In addition, records have been maintained for fifteen to twenty years of temperature and salinity in the north-central part of the Sound, oyster spawning and setting, and other oceanographic matters of both practical and scientific interest.

In 1938 the Bingham Oceanographic Laboratory began a year's survey of plankton and associated environmental factors in the same area (RILEY, 1941), and similar work was carried on during the summers of 1940, 1941, and 1950. A program of broader scope was instituted in 1952, consisting of weekly coverage of a grid of stations in the central part of the Sound for a two-year period, followed by a further expansion to coverage of the Sound as a whole at approximately monthly intervals. The latter work is still in progress.

The present paper reviews some of the work that has been done and attempts to extract some ecological generalizations that will be applicable to Long Island Sound in particular and perhaps in some cases to temperate littoral waters in general. For purposes of comparison it is pertinent to mention other work in nearby waters: a survey of temperature and salinity distribution by the Woods Hole Oceanographic Institution in the area from Woods Hole to the central part of Long Island Sound in 1946, a study of Block Island Sound from 1943 to 1946 and in 1949 by the Bingham Oceanographic Laboratory, and the work of RYTHER (1954) and other Woods Hole staff members in the bays on the south shore of Long Island.

PHYSIOGRAPHY AND PHYSICAL OCEANOGRAPHY

Long Island Sound (Fig. 1) is a semi-enclosed body of water some 90 nautical miles long, with a maximum width of about 15 mi. and an area of 928 sq. mi. The maximum depth in the eastern end is about 100 m. There is little water of more than 35 m in the central and western basins, and the mean depth of the Sound as a whole is only 20 m. Free interchange with the waters of Block Island Sound occurs through a series of passes at the eastern end. In the west there is more limited interchange with the New York harbour and river waters.

The drainage basin is roughly eleven times the area of the Sound, and the annual volume of freshwater drainage averages 35% of the volume of the Sound. However, three-quarters of the river water enters the relatively open eastern end, where it is flushed out rapidly and has a minimal effect on the Sound as a whole.

Tidal interchange totals 8·6% of the volume of the Sound below mean low water, leading to currents of three knots or more in the eastern passes and a maximum speed

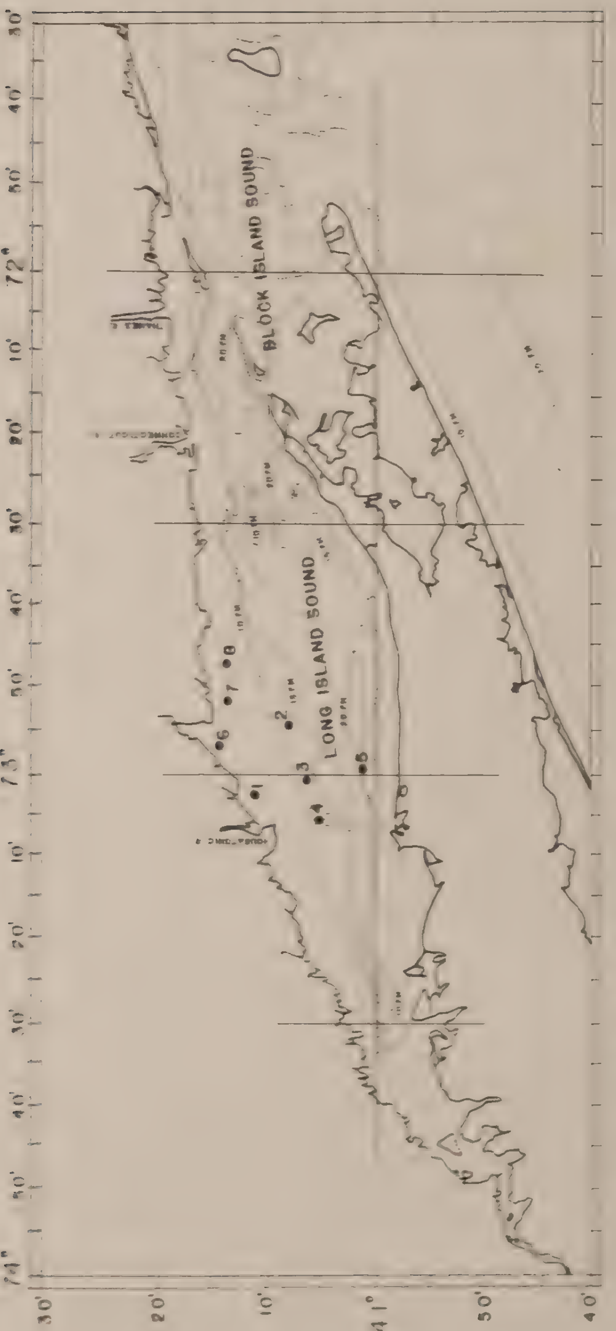
30'
40'
50'
72°
10'
20'
30'
40'
50'
73°
10'
20'
30'
40'
50'
74°
30'
20'
10'
41°
50'
40'
BLOCK ISLAND SOUND
LONG ISLAND SOUND
1
2
3
4
5
6
7
8

Fig. 1. Chart of Long Island Sound and adjacent waters. Depth contours at 10, 15, and 20 fm. in the Sound, 10 and 20 fm. elsewhere. Routine station positions of the 1952–54 survey in the central part of the Sound are shown as numbered dots.

of about one knot in the central and western basins. Many current stations, particularly in the eastern part of the Sound, show that the ebb is stronger than the flood in the surface layer, while the reverse is true at the bottom. Thus there is a tendency here, as in many other sounds and estuaries, for the surface layer to move seaward and to be replaced by saline water flowing in along the bottom. An analysis of the available current stations during the summer season (Riley, 1955 a) indicates that this inflow through the eastern passes is of the order of 15–20 thousand m^3 per second. The bottom transport decreases rapidly as it moves west, approaching zero near the western end of the Sound. Clearly the slowing down is due to upwelling of bottom water and admixture with the surface layer, and current measurements demonstrate a corresponding augmentation of the eastward surface transport. The calculated mean rate of upwelling required to satisfy the principle of mass continuity is small, ranging from about 5 cm per month in the central and western part of the Sound to a maximum of 45 cm in the vicinity of the passes.

It would appear from current stations that about 1,100 m^3/sec enter the western end of the Sound from New York harbour and flow eastward as part of the surface layer. The latter is further augmented by freshwater drainage, amounting to about 300 m^3/sec in summer. Thus the surface outflow at the eastern end should exceed the inflow by about 1,400 m^3/sec, although the statistically derived transport estimates are not accurate enough to demonstrate this.

Complete current surveys are available only for the summer period. Analyses of salt balance (Riley, 1952 a) indicated a seasonal variation correlated with freshwater drainage. Surface current measurements at Bartlett Reef Lightship in the eastern end of the Sound (Le Lacheur and Sammons, 1932) showed a similar relationship, but farther west, at Cornfield Lightship, the seasonal variation was slight and was not clearly correlated with river outflow.

The distribution of temperature and salinity has been described by Galtsoff and Loosanoff (1939) and Riley (1952 a). Surface water temperatures have a seasonal range of roughly 3° to 19° in the eastern end of the Sound and 0° to 23° in the western portion. The total salinity range is about 23 to 31 $^{\circ}/_{\circ\circ}$, excluding occasional eddies of fresher water in the immediate vicinity of the rivers. The east–west salinity gradient is ordinarily about 5 $^{\circ}/_{\circ\circ}$, and there is a seasonal variation of 2 to 4 $^{\circ}/_{\circ\circ}$.

A two-year series of observations in the central part of the Sound (Riley, 1955 a) at station positions shown in Fig. 1 serves to illustrate general features of the temperature and salinity cycles. There was a small thermocline in spring and summer, and the maximum difference between surface and bottom temperature was about 5° (Fig. 2). A slight salinity gradient was maintained throughout most of the year by the combined effects of freshwater dilution of the surface layer and inflow of saline water along the bottom. Differences in the seasonal cycles from one year to the next show obvious correlations with the meteorological variables included in Fig. 2.

SEASONAL CYCLES OF PLANKTON AND CHEMICAL FACTORS

The upper part of Fig. 3 shows the seasonal cycles of surface and bottom phosphate and nitrate as averages of analyses at inshore stations 1, 6, 7, and 8 (Riley and Conover, 1955). Chlorophyll analyses included in the figure provide an estimate of the total phytoplankton population, and zooplankton catches obtained by oblique tows with a Clarke–Bumpus sampler are plotted as total displacement volumes.

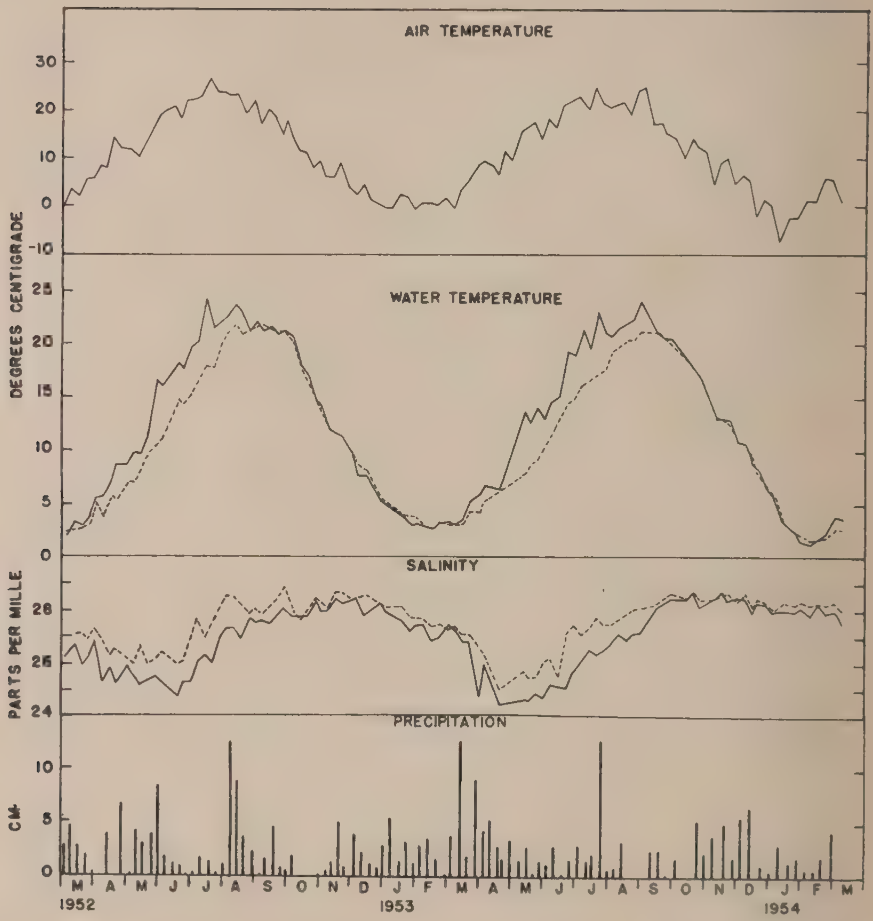

Fig. 2. Average temperature in °C and salinity in parts per mille at the surface (solid lines) and bottom (dotted lines) at offshore stations 2 to 5 (cf. Fig. 1). Weekly averages of air temperature recorded by the New Haven Weather Bureau and total precipitation in cm between successive dates of oceanographic observation.

The gross features of nutrient cycles are characteristic of temperate waters, but the proportions of nitrate–nitrogen and phosphorus are anomalous. During the winter maxima, the ratio of N:P by atoms has been of the order of 8:1, about half the value that might be expected in oceanic waters. The late winter flowerings of 1953 and 1954 almost completely exhausted the supply of nitrate in about three weeks but left a residuum of about 0·5 μg-at of phosphate-P in the water.

Most of the spring and summer analyses have shown little or no nitrate in any part of the water column. HARRIS (unpublished) has found small but significant quantities of ammonia, and this, together with organic nitrogen compounds, constitutes the main source of supply. Phosphate values during the same period generally have been within the range of 0·2 to 1 μg-at P per litre. Phosphate tended to increase gradually during the summer and more rapidly in autumn. Nitrate remained low

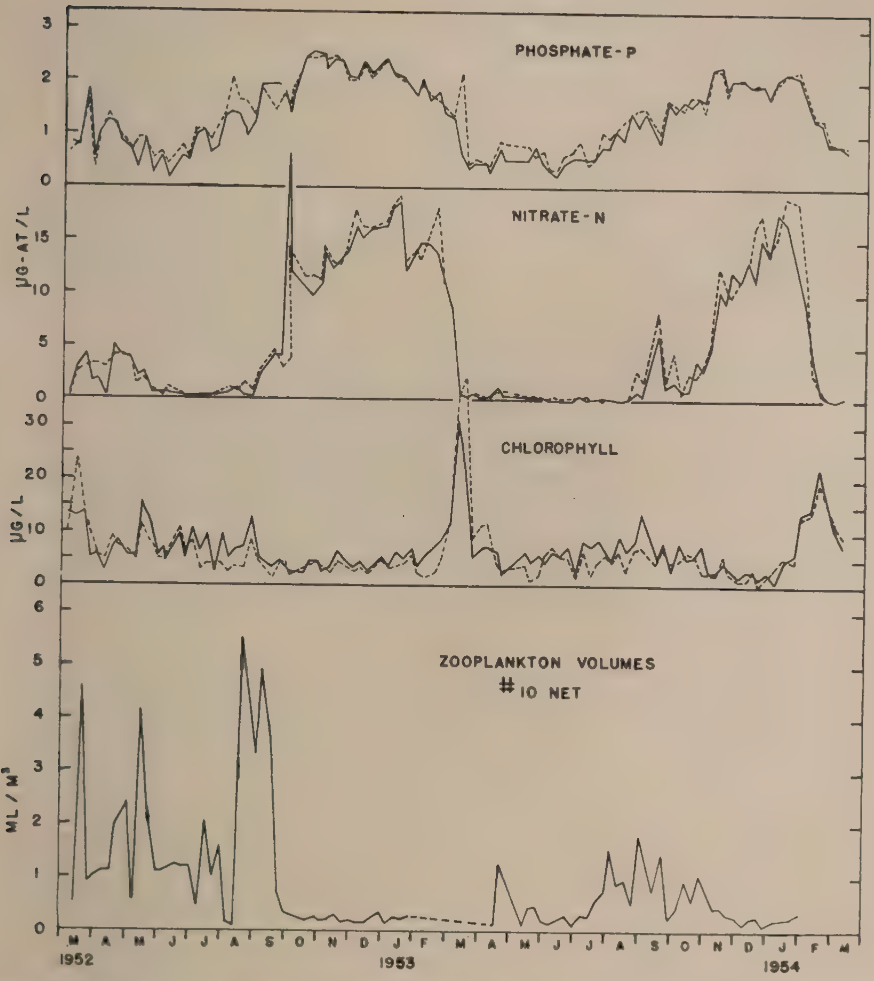

Fig. 3. Average phosphate, nitrate, and chlorophyll at the surface (solid lines) and bottom (dotted lines) at inshore stations 1, 6, 7 and 8. Zooplankton displacement volumes, also at inshore stations, are averages for the water column obtained by oblique tows with a No. 10 net.

until September. The autumn increase in nutrients was interrupted in October, 1953, presumably because of plant growth. While there was not a pronounced autumn flowering in the ordinary sense of the term, both phytoplankton and zooplankton crops were larger than in the autumn of 1952.

Phosphate and nitrate increased slightly from surface to bottom during most of the spring and summer. Stability was too slight to permit the accumulation of a large store of regenerated nutrients in the bottom water. It was reasonable, then, to find neither a pronounced summer period of phytoplankton impoverishment nor a marked flowering following destruction of the summer thermocline. It was common in autumn and early winter to find a significant reduction in phosphate and nitrate in the bottom water. The reason for this peculiar phenomenon will be discussed later.

The major diatom flowering occurred in late winter, as previously reported in Long Island Sound (RILEY, 1941) and some other littoral waters off the New England coast (BIGELOW, 1926; FISH, 1925). An early flowering in these latitudes requires that the phytoplankton be confined to a shallow stratum, since it is only in such an environment that the effective light intensity in winter exceeds the threshold necessary for active growth. Hence the flowering is likely to be early in shallow water and to begin later in the deeper water, frequently only after the establishment of vernal stability (BIGELOW, LILLICK, and SEARS, 1940; RILEY, 1942). In a particular location the time of the flowering may vary from year to year in accordance with variations in the amount of light available (ATKINS, 1928). However, in comparing the winters of 1953 and 1954 in Long Island Sound, there were no marked differences in incident radiation, and another explanation must be sought for the fact that the 1954 flowering was about three weeks earlier.

S. CONOVER (1955) found that the midwinter diatom population was dominated by two species, *Skeletonema costatum* and *Thalassiosira nordenskiöldii*, in about equal proportions. In 1953 *Skeletonema* dominated the flowering, achieving an average concentration of 36 million cells per litre at the stations sampled on March 9, as compared with one million cells per litre of *Thalassiosira*. In 1954 *Thalassiosira nordenskiöldii* rose to six million cells per litre on February 17, while *Skeletonema* achieved a peak concentration of nine million cells the following week. Considering the difference in size of the two species, *Thalassiosira* clearly dominated the early flowering period in 1954.

CONOVER conducted a series of experiments in 1954 in which natural populations were bottled and treated to a variety of conditions of light, temperature and nutrient enrichment. Table I shows a part of the data from the experiment of February 10 that is pertinent to the present discussion. It is apparent that *Thalassiosira* has an optimum growth rate at low temperatures and can tolerate low light intensities, while *Skeletonema* requires higher temperature and probably better illumination. Later experiments suggested that the critical temperature determining which species will dominate is between 2·4 and 3·7 °C. The mean temperature in the Sound was 3·2° in February 1953, and 3·7 in March, and the corresponding means for 1954 were respectively 1·7 and 3·5 . CONOVER concluded that the lower temperature in 1954

Table I

Growth coefficients (fractional increase in cell number per day) of Skeletonema costatum *and* Thalassiosira nordenskiöldii *in two-day experimental exposures of natural surface water phytoplankton populations to normal seasonal temperature and surface light intensity, to reduced light, and to increased temperature*

Temperature ° *C*	*Growth coefficients* *Skeletonema*	*Thalassiosira*
1·7	–0·021	0·058
1·7*	–0·025	0·015
5·0	0·144	–0·133
8·0	0·258	–0·163

* Average of four experiments at light intensities ranging from 1 to 24% of the surface value.

favoured the dominance of *Thalassiosira* and that its tolerance to low light intensity permitted a relatively early flowering. Contrariwise, physical conditions promoted dominance by *Skeletonema* throughout February and March, 1953, and toward the end of the 1954 flowering.

In 1955 the flowering was even earlier. The major growth took place during the last ten days of January, and the peak was attained early in February. The New Haven Weather Bureau reported that the percentage of sunshine in January, 1955, was the highest that has been recorded in 55 years of observation, so that an early flowering was not unreasonable. The temperature in the Sound was 3·1 to 3·3° at the beginning of the flowering, and *Skeletonema* was the dominant species. As the flowering progressed the temperature dropped to about 1°. At this writing, counts of the phytoplankton for this period have not been completed. Preliminary indications are that *Thalassiosira* gained in relative importance but was unable to achieve complete dominance.

Experiments by S. Conover (1955) showed that the 1954 flowering was terminated largely because of nitrogen deficiency. At this time and again in June, 1954, natural phytoplankton populations were enriched with phosphate, nitrate, iron, and manganese, singly and in combination. In all cases nitrogen was the one element that had a significant effect on the population as a whole, although individual species occasionally responded to other types of enrichment. Nevertheless, the percentage of nitrogen in the phytoplankton remained nearly constant through the year (Harris and Riley,

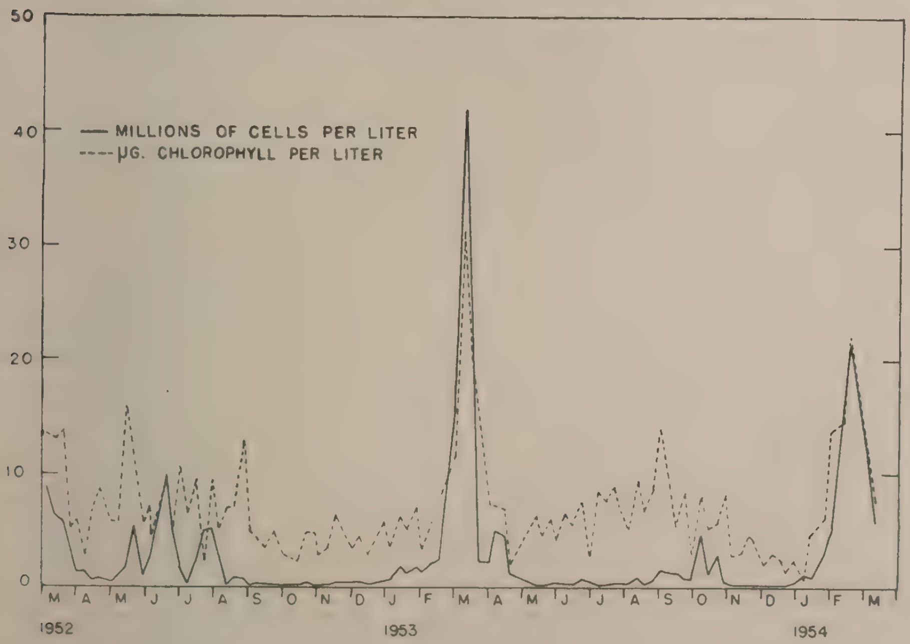

Fig. 4. Phytoplankton cell numbers and chlorophyll concentrations in the surface waters, plotted as the average of all values obtained at inshore stations.

1955), so that the deficiency obviously does not approach the extremity of laboratory cultures, in which the nitrogen content may be reduced to one-third normal (KETCHUM and REDFIELD, 1949).

It is beyond the scope of this paper to discuss seasonal succession in detail, but one other major feature is apparent in Fig. 4, which compares chlorophyll analyses with CONOVER's cell counts. The latter comprised mainly diatoms and armoured flagellates. In addition, occasional examinations of fresh material in summer have revealed two to five million naked flagellates per litre and many millions of small, unidentified *Chlorella*-like cells. These small species are believed to be largely responsible for the disparity between chlorophyll and routine cell counts in summer. Long Island Sound seems to resemble, to a much less extreme degree, the situation described by RYTHER (1954) in Great South Bay and Moriches Bay, Long Island, where there was an excessive summer dominance by " small forms ". These were shown by RYTHER's experiments to be favoured in their competition with diatoms by reduced salinity, high temperature, a low N:P ratio, and the presence of nitrogen primarily in forms other than nitrate. Similar environmental tendencies have been noted in Long Island Sound. It is perhaps significant in this connection that the slightly higher nitrate values during the summer of 1952 were accompanied by much larger quantities of diatoms.

In the locality described by Ryther, the nannoplankton appeared to have a distinctly toxic effect on shellfish. There is no evidence of a similar situation in the Sound. LOOSANOFF *et al.* (1947; 1953) have studied feeding rates and toxicity reactions of lamellibranchs, using a variety of nannoplankton species as food organisms. Their work indicates that the concentration of organisms required for toxic effects is well above the level of the population found in the Sound. On the other hand, R. CONOVER (1955) found that *Acartia*, the dominant genus of copepods in these waters, feeds much more effectively on diatoms than on nannoplankton. Hence the value of the latter as zooplankton food is somewhat questionable.

Quantitative aspects of the total zooplankton population, as depicted in Fig. 3, provide little material for generalization except that there is a minimal population in autumn and early winter, a larger but rapidly fluctuating crop in spring and summer, and a vast difference from one year to the next. Similar variability in the level of the summer population has been noted in previous studies during the summers of 1938 to 1941. There is no satisfactory explanation, although it may be argued on rather tenuous grounds that a causal relation exists between the relative abundance of nitrate, diatoms and zooplankton in 1952 as compared with their scarcity the following year.

According to DEEVEY (1955), copepods are the dominant zooplankton organisms in the Sound, the most important species being *Acartia clausi* and *A. tonsa*, with smaller but significant quantities of *Temora longicornis*, *Pseudocalanus minutus*, *Paracalanus crassirostris*, and *Oithona* spp. Several other copepods and three species of Cladocera occasionally constituted as much as 5% of the population, as did the larvae of various bottom invertebrates. In general, the species composition was quite limited, and several species that are common in the outer coastal waters and are known to have a wide salinity tolerance were unable to maintain significant numbers in the Sound.

R. CONOVER (1955) has made a descriptive and experimental study of the two species of *Acartia* with particular reference to problems of seasonal succession. *A. clausi* appeared in November or December and increased to a maximum in May of

102,000 per m³ in 1952 and 62,000 in 1953. A rapid decline followed, and the species disappeared from the water in early August. *A. tonsa* appeared in June and increased to 82,000 per m³ in August, 1952 and 46,000 in 1953. There was a more or less steady decrease during the autumn and early winter, a slight rise in early spring, and then virtual disappearance from the water. Thus *A. clausi* was dominant in winter and spring and was replaced by *A. tonsa* in summer and autumn, but both species persisted through almost the entire seasonal temperature range.

The data did not completely rule out the possibility that seasonal succession is controlled by direct, lethal temperature effects, but the form of the seasonal cycle suggested the more likely possibility of a temperature controlled inter-species competition. During the winter, when *A. clausi* was replacing *A. tonsa*, the latter was found mainly in the bottom waters. In laboratory experiments at low temperature, it was sluggish, but mortality was not excessive. The possibility of temperature-controlled competition was explored through the medium of grazing and respiratory experiments. The grazing experiments determined the quantity of water that each species could filter in a given length of time, and this, combined with the observed quantity of phytoplankton in the Sound, provided an estimate of total food intake. Respiratory experiments in turn determined how much of the food intake was required to satisfy immediate metabolic needs. In *A. tonsa* these two quantities were about equal during most of the winter. Only at the time of the flowering did the intake appear to be substantially larger than the requirement. *A. clausi*, on the other hand, was able to feed at a materially higher level than its rate of metabolic loss throughout the winter and hence was a favoured competitor for food at this season.

In summer *A. tonsa* was found in greatest abundance near the surface and *A. clausi* in the slightly cooler bottom layer, so that there was no close and immediate competition for food. Despite the preference for low temperature, *A. clausi* also remained a more effective feeder in summer than *A. tonsa*. Thus the summer succession involved a different mechanism, and one which has not been worked out in detail. But since adult *A. clausi* remained in the Sound for some time after immature stages disappeared, Conover concluded that the replacement was due either to failure of the animals to reproduce at high temperatures or to competition among the juveniles.

HORIZONTAL DISTRIBUTION OF PLANKTON AND NUTRIENTS

Maximum concentrations of both phytoplankton and zooplankton are ordinarily found in the western end of the Sound and in the shallow waters along the north shore. Here the average concentration of phytoplankton is about three times as large as in the eastern end of the Sound or in Block Island Sound and ten times the concentration in the outer coastal waters. Horizontal gradients in zooplankton and nutrients are similar but not so extreme.

Maximum concentrations are found in very shallow water, and the differences in the total population underlying a unit area of surface are not so marked. Ratios of the total populations in the Long Island and Block Island Sounds average about 1·5:1 for phytoplankton and 1:1 for zooplankton.

It has often been stated that inshore waters are very fertile and that this is primarily due to enrichment by freshwater drainage. However, it is apparent that there are no large regional differences in the total plankton population in southern New England waters, nor is there evidence of much difference in rates of production. Methods of measuring the latter are not accurate enough for precise estimates, but such information as is available (RILEY, 1952 B and 1955 C) indicates little difference between the Long Island and Block Island Sounds as far as phytoplankton productivity is concerned.

To be sure, Long Island Sound maintains a slightly higher concentration of nutrients, although again not necessarily a larger total stock per unit area. Two factors tend to maintain this higher concentration. First, freshwater drainage contains a highly variable but generally higher concentration of nitrate (but not phosphate) than Sound waters. Secondly, two-layered transport exchange creates a mechanism whereby the biological system automatically regulates the nutrient supply at a slightly higher level than in the outside waters. During most of the spring and summer, plant growth is sufficiently active to impoverish the nutrient supply in the surface layer. Part of the phytoplankton produced at the surface is utilized elsewhere in the water column, as is sufficiently evident from the existence of a bottom fauna. Thus the surface layer that is transported out of the Sound is relatively poor in total nutrient content, and the latter tends to be conserved and concentrated within the Sound as long as plant growth is sufficiently active to maintain a vertical gradient in nutrients.

During the autumn, when regeneration of nutrients exceeds utilization, very large concentrations have been found toward the western end of the Sound. These tend to be reduced as the season progresses by the combined effects of lateral diffusion and transport exchange. It has been common in autumn and early winter to find positive vertical gradients in nutrients, where rich western water overrides the inflowing bottom water. It was the frequency of this rather unusual type of vertical distribution that first focussed attention on the subject.

Preliminary calculations of enrichment by transport exchange have been made, using transport data mentioned earlier and the observed distribution of phosphate and nitrate. The amount of enrichment in the western half of the Sound during the spring–summer season was estimated to equal one-third of the amount of phosphate present at the time of the midwinter maximum and one-tenth of the nitrate stock. More accurate evaluation of this problem, and of the relative importance of river drainage, awaits the completion of work in progress on seasonal variations in the exchange rate and the distribution of total as well as inorganic nutrient stocks.

ORGANIC PRODUCTION

Two one-year series of measurements have been made of the photosynthetic rate of the surface phytoplankton in Long Island Sound (RILEY, 1941; S. CONOVER, 1955) using the light and dark bottle technique. The later work also included a few measurements at a series of depths from surface to near bottom. Another type of analysis has also been used to estimate the biological rate of change of oxygen and phosphate at various levels in the water column and on the bottom (RILEY, 1955 C). Having determined coefficients of vertical eddy conductivity from the vertical distribution and seasonal change in temperature, the coefficients were then applied to the observed distribution of oxygen and phosphate. This provided information on the rate of accumulation or depletion of the element at a given depth by vertical mixing. Any difference between the calculated rate and the observed change was then ascribed to biological processes. The oxygen and phosphate analyses agreed within narrow limits. The calculated net rate of change of oxygen in the surface layer was about 50% larger than the increase in experimental light bottles. The discrepancy may have been due to experimental error, since it is well known that bacterial growth is abnormally large in bottled sea water. However, there are also several possible sources of error in the physical oceanographic calculations, so that there is an uncertainty factor of at least 50% in the results of the productivity compilation.

The consumption of organic matter by the benthic community was estimated by physical oceanographic computation of the rate of transfer of oxygen downwards through the lower few metres of water and by the rate of upward transfer of phosphate from the bottom. An estimate of the rate of consumption by the plankton community could be obtained from the net rate of utilization of oxygen in the lower part of the water column, since the vertical distribution of plankton was relatively uniform. However, it was a minimal estimate because experiments showed a slight but significant amount of photosynthesis at depths of 15 to 20 m in summer. Dark bottle respiration averaged approximately twice the net rate of change in the lower water column. Experimental values were presumably too high, and therefore an intermediate value was chosen to represent the total oxygen consumption of the plankton community. Results are shown in Table II, together with somewhat similar estimates by HARVEY (1950) for the English Channel.

Table II

Comparison of mean annual standing crops and organic production (grams organic matter per m²) in the English Channel (EC) and central Long Island Sound (LIS)

	Standing crop		*Daily production*		*Daily loss by respiration*	
	EC	LIS	EC	LIS	EC	LIS
Phytoplankton	4	16	—	3·2*	—	1·8*
			0·4–0·5†	1·07†		
Zooplankton	1·5	2	0·15	—	0·06	0·28
Pelagic fish	1·8	—	0·0016	—	0·025	—
Bacteria	0·04	—	—	—	0·013	0·46‡
Demersal fish	1–1·25	—	0·001	—	0·015	0·33
Epi- and in-fauna	17	19–38	0·03	—	0·2–0·3	
Bacteria	0·1	—	—	—	0·03	
Total consumption, exclusive of phytoplankton respiration					0·34–0·44	1·07

* Photosynthetic glucose production and loss of glucose by respiration.
† Production of phytoplankton of normal organic content in excess of respiratory requirement.
‡ Includes bacteria and microzooplankton. For further explanation of this item see text.

Data for the English Channel were obtained at a station in 70 m of water off Plymouth, as compared with a mean depth of 20 m in Long Island Sound. Nutrient concentrations were relatively low in the English Channel, although the total stock in the water column at the time of the winter maximum was about the same in both areas.

The Sound has a larger standing crop of phytoplankton and greater basic productivity. The zooplankton crop is only slightly greater. In this connection, R. CONOVER (1955) has pointed out that the dominant copepod *Acartia* is a relatively inefficient feeder, has a remarkably high respiratory requirement, and probably achieves great dominance only in waters that are sufficiently brackish to exclude the more efficient oceanic forms.

The estimate of zooplankton respiration is based on Conover's work, and the phytoplankton respiratory rate is a compilation of field and laboratory data by RILEY, STOMMEL, and BUMPUS (1949). When these items are subtracted from the total estimated respiration in the water column, the remainder, representing 0·46 g of organic matter consumed per day, is ascribed in Table II to bacteria and the fraction of small zooplankton that is not captured by the Number 10 net. While both of these elements of the population appear to be important, it is apparent that the method of calculation allows a wide margin of possible error in the estimate.

Consumption on the bottom in Long Island Sound appears to be about the same as HARVEY's total, although collections of benthic invertebrates in the Sound (Sanders, in preparation) are larger. Later work in the English Channel by HOLME (1953) tends to reduce HARVEY's estimate, so there is little doubt that the Sound has a larger total biomass. The number of animals is enormous, and the mean size of the individual is small compared with the English Channel.

WHEATLAND (1955) has demonstrated that the Sound is an important spawning and nursery ground for several species of fish. Little work has been done on adult fishes, but the commercial catch is small, and WHEATLAND's examination of catch statistics indicated that the catch per unit effort is smaller than in the adjacent Block Island Sound.

In short, the high basic production in Long Island Sound is utilized by great numbers of small animals. Conversion to high-level food chain carnivores appears to be relatively inefficient.

GENERAL DISCUSSION OF FOOD CHAIN EFFICIENCY

Block Island Sound has a net production (excess of photosynthesis over respiration of the phytoplankton) estimated by RILEY (1952 B) at 285 grams of carbon per square metre of sea surface in a year, as compared with 205 grams in Long Island Sound. However, a considerable fraction of phytoplankton appeared to be lost by horizontal dispersal into the outer coastal region and the amount utilized *in situ* by the biological association was estimated to be only 150 grams. The annual fish production in Block Island Sound is about 50 to 100 lb. per acre wet weight (estimated from data in MERRIMAN and WARFEL, 1947). In terms of carbon content, this amounts to between 0·4 and 0·8% of the net phytoplankton production. From Table II it may be seen that Harvey's estimate of the combined pelagic and demersal fish production in the English Channel is 0·52 to 0·65% of the phytoplankton production. Hence both areas have about the same level of efficiency in food chain conversion, although Block Island Sound is more productive in the absolute sense.

Phytoplankton production on Georges Bank also nets about 150 grams of carbon per year (RILEY, 1944). Commercial fish catches have ranged from 7 to 33 lb. per acre, according to CLARKE (1946). Total production is probably more than twice the landings of table fish, so that the efficiency level is not very different from the figures listed for Block Island Sound and the English Channel.

A very different situation is found in such areas as the Sargasso Sea. Here the level of net production is uncertain, recent estimates varying from 30 g carbon per m² per year (STEEMANN NIELSEN, 1952) to 110 g (RILEY, 1953). According to RILEY, STOMMEL and BUMPUS (1949), the total displacement volume of zooplankton underlying a square metre of sea surface is equal to the amount found on Georges Bank or in the Gulf of Maine and double the crop in southern New England coastal waters. However, its organic content is very low, and it was suggested that the zooplankton is a starved population, possibly with a low rate of production. The extended disposition of the plankton through a long vertical column in such waters requires the expenditure of a relatively large amount of energy in food capture and theoretically should lead to inefficiency in food conversion, with progressive attenuation of the higher members of the food chain. Quantitative information on the total fish population is lacking, but there is no evidence to indicate that it is a large one. Thus the basic production is roughly of the order of magnitude of that found in the English Channel, but it is largely dissipated at the plankton level.

It would appear that a high level of plant production is necessary but not sufficient for a thriving fishery. Block Island Sound and Georges Bank are probably superior to the English Channel at all levels of the food chain, but the English Channel appears to produce more marketable fish than Long Island Sound despite the high basic production of the latter.

Optimum efficiency of conversion seems to be characteristic of coastal and bank waters of moderate depth and salinity of 30°/₀₀ or more. A lesser degree of efficiency is probably to be expected in most deep oceanic waters. Two examples of brackish waters that have been examined, namely Long Island Sound and the Moriches–Great South Bay area, although productive in the basic sense also seem to be relatively inefficient in food chain conversions. The underlying reasons for this are not clearly understood, although some of the symptoms are obvious. There is a large proportion of nannoplankton existing in an environment which, according to RYTHER'S (1954) experimental studies, favours the dominance of such forms. They are not particularly good food for the large zooplankton which in turn would be the major source of food for larger animals. The brackish environment also apparently favours the dominance of zooplankton species that are inefficient feeders. Thus there exists in the water a relatively large quantity of unutilized phytoplankton and organic detritus. This in itself is a clear symptom of a low rate of turnover, and it probably promotes the dissipation of a major fraction of the energy of the system at low levels by bacteria and microzooplankton. It also tends to produce a bottom sediment of high organic content. The latter generally supports a smaller biomass than a mixed sand and mud bottom and one that is qualitatively less desirable for benthic carnivores. The mud bottoms in Long Island Sound have enormous numbers of nematodes and other microfauna which presumably have a high food requirement and rate of production but are of very limited value as food for groundfish.

REFERENCES

ATKINS, W. R. G. (1928), Seasonal variation in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *J. Mar. Biol. Assoc.*, U.K., n.s., **15**, 191–205.

BIGELOW, H. B. (1926), Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 1–509.

BIGELOW, H. B., LILLICK, L. C. and SEARS, MARY (1940), Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. I. Numerical distribution. *Trans. Amer. Phil. Soc.*, **31** (3), 149–191.

CLARKE, G. L. (1946), Dynamics of production in a marine area. *Ecol. Monogr.*, 16 (4), 321–335.

CONOVER, R. J. (1955), Oceanography of Long Island Sound, 1952–54. VI. Biology of the copepod genus *Acartia*. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

CONOVER, S. M. (1955), Oceanography of Long Island Sound, 1952–1954. IV. Phytoplankton. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

DEEVEY, G. B. (1955), Oceanography of Long Island Sound, 1952–1954. V. Zooplankton. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

FARLOW, W. G. (1879), The marine algae of New England. *U.S. Comm. Fish and Fish.* VII. *Rept. for* 1879, 1–120.

FISH, C. J. (1925), Seasonal distribution of the plankton of the Woods Hole region. *Bull. U.S. Bur. Fish.*, **41,** 91–179.

GALTSOFF, P. S. and LOOSANOFF, V. L. (1939), Natural history and method of controlling the starfish (*Asterias forbesi*, Desor). *Bull. U.S. Bur. Fish.*, **49**, 75–132.

HARRIS, EUGENE and RILEY, G. A. (1955), Oceanography of Long Island Sound, 1952–54. VIII. Chemical composition of the plankton. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

HARVEY, H. W. (1950), On the production of living matter in the sea off Plymouth. *J. Mar. Biol. Assoc.*, U.K., n.s., **29,** 97–137.

KETCHUM, B. H. and REDFIELD, A. C. (1949), Some physical and chemical characteristics of algae growth in mass culture. *J. Cell. Comp. Physiol.*, **33**, 281–299.

LELACHEUR, E. A. and SAMMONS, J. C. (1932), Tides and currents in Long Island and Block Island Sounds. *U.S. Coast Geod. Surv., Spec. Publ.*, **174**, 1–184.

LOOSANOFF, V. L. and ENGLE, J. B. (1947), Effect of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). *Fish. Bull., U.S. Fish Wildlife Serv.*, **51**, 29–57.

LOOSANOFF, V. L., DAVIS, H. C. and CHANLEY, P. E. (1953), Behavior of clam larvae in different concentrations of food organisms. *Anat. Rec.*, 117, 586–587.

MERRIMAN, DANIEL and WARFEL, H. E. (1947), Studies on the marine resources of southern New England. VII. Analysis of a fish population. *Bull. Bingham Oceanogr. Coll.*, **11** (4), 131–163.

RILEY, G. A. (1941), Plankton studies. III. Long Island Sound. *Bull. Bingham Oceanogr. Coll.*, **7** (3), 1–93.

RILEY, G. A. (1942), The relationship of vertical turbulence and spring diatom flowerings. *J. Mar. Res.*, **5,** 67–87.

RILEY, G. A. (1944), The carbon metabolism and photosynthetic efficiency of the earth as a whole. *Amer. Scient.*, **32,** 129–134.

RILEY, G. A. (1952 A), Hydrography of the Long Island and Block Island Sounds. *Bull. Bingham Oceanogr. Coll.*, **13** (3), 5–39.

RILEY, G. A. (1952 B), Phytoplankton of Block Island Sound, 1949. *Bull. Bingham Oceanogr. Coll.*, **13** (3), 40–64.

RILEY, G. A. (1953), Letter to the Editor. *J. du Cons.*, **19,** 85–89.

RILEY, G. A. (1955 A), Oceanography of Long Island Sound, 1952–54. II. Physical oceanography. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

RILEY, G. A. (1955 B), Oceanography of Long Island Sound, 1952–54. IX. Production and utilization of organic matter. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

RILEY, G. A. and CONOVER, S. M. (1955), Oceanography of Long Island Sound, 1952–54. III. Chemical oceanography. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

RILEY, G. A., STOMMEL, HENRY and BUMPUS, D. F. (1949), Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bingham Oceanogr. Coll.*, **12** (3), 1–169.

RYTHER, J. H. (1954), The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.*, **106,** 198–209.

SANDERS, H. L. *The Bottom Fauna of Long Island Sound.* In preparation.

STEEMANN NIELSEN, E. (1952), The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J. du Cons.*, **18,** 117–140.

VERRILL, A. E. (1873), Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *U.S. Comm. Fish and Fish.* I. *Rept. for* 1871–1872, 295–778.

WHEATLAND, S. B. (1955), Oceanography of Long Island Sound, 1952–54. VII. Pelagic fish eggs and larvae. *Bull. Bingham Oceanogr. Coll.*, **15** (1). In press.

Papers in Marine Biology and Oceanography. Suppl. to vol. 3 of Deep-Sea Research, pp. 239-241.

Development and metamorphosis of the larva of *Agalma elegans* (Sars) (Siphonophora Physonectae)

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Although Fewkes (1885) published a detailed and illustrated account of the holoblastic segmentation of the eggs of *Agalma elegans*, and of the subsequent development of the larva till it surfaces at the age of about seven days, he did not follow its metamorphosis into the adult. He had previously, however, given (1881, pl. IX, Figs. 1, 2) rather inadequate figures of a post-larval *Athorybia* stage, and a later one that he called the *Physophora* stage. The last is perhaps better called the " *Nectalia* " stage, as I have suggested (1954, p. 62).

Metchnikoff (1874) had, before Fewkes, watched segmenting eggs of this species without figuring them. He also gave an account, though not so good a one as Fewkes, of the development of the larva and the initial stage of its metamorphosis. But it is difficult to interpret Metchnikoff's later figures and to discriminate between the categories of buds that he figured.

Haeckel (1869) had been the first to describe the development of an Agalmid, after he had artificially raised about 60 larvae (one of them to the 27th day) of *Agalma okenii* (*Crystallodes rigidum*) at Lanzarote. He did not recognize the first gastrozooid or protozooid as such. It is labelled " d " (Dotter) and " dc " (Dotterhöle) in all his figures, whilst his Magen-polyp (" p ") is really the second gastrozooid. He did not figure a larval tentacle for the protozooid, and I have never seen one either in *Agalma okenii*. In my *Discovery* report (1954, p. 66) I noted that the terminal gastrozooid—the primary zooid or protozooid—was smaller in *Agalma okenii* than its successors, and had a reduced basigaster. On page 69, however, I made the erroneous statement that such a protozooid was not formed. The sentence (lines 11–14) " The explanation . . . *okenii* " should be deleted.

Reduction of the protozooid in *Agalma okenii* has gone further than in *Agalma elegans*, whilst evolution of the bracts has progressed, giving the whole bud-colony a character of its own.

Adult specimens of *Agalma elegans* were not available except on one day during three visits that I have paid to Villefranche, and I was not able to secure any of the very youngest larvae, either by attempts at breeding or in the tow-net; but I did collect large numbers of post-larvae in various stages of development, and can now complete the account of growth and metamorphosis.

The fate of the larval bracts of the *Athorybia*-like stage has been unknown. Garstang (1946) several times suggested that they are dropped at metamorphosis. As a fact they, or at any rate the last-developed ones, are retained through life in their original very restricted position surrounding the proximal sides of the first and second gastrozooids to appear, where they can be seen figured by Fewkes (1881, pl. IX, Fig. 1) and by Totton (1954, frontispiece, Figs. A, D). But because of the secondary elongation of the area between the budding zone (blastocrene) of the siphosome and the bases of the first two gastrozooids, the area which bears these bracts takes up a subterminal position at the end of a long stem. These larval bracts, so often figured, and their successors of similar though slightly modified shape, are quite distinctive; and differ from the definitive bracts, which arise in hundreds proximally to them in several ventro-lateral meridians of the stem. The contrast in bracteal types is best seen in early stages of metamorphosis, when the definitive bracts first make their appearance.

Information has been wanting in published reports on the position and time of first appearance of the nectophores. Garstang suggested that, as the nectophores appeared, so the bracts, which hitherto had served for locomotion, dropped off, but as we have seen this is not so. The oldest of Metchnikoff's figured specimens, in what might be called the *Melophysa* stage of development, shows two functional nectophores, but unless the reader is familiar with the animals it is not easy to orientate and interpret the figure. The little group of four rounded buds, seen through the uppermost bract, probably represent buds of gastrozooids and palpons. Close by, though not figured, is the nectostyle to which the larval bracts are attached by their muscular lamellae. The nectostyle can be seen in sagittal section (Fig. 1A) to be an elongated, hollow, cone-shaped diverticulum of the general cavity. The larval bracts are attached by muscular lamellae at different levels on many meridians on either side of the ventral line from which the cormidia are budded. From the opposite side of the pneumatophore spring the nectophores. As pointed out by Garstang (1946), delamination of tissues starts on one side (called ventral, on which the nectostyle is found), and proceeds gradually towards the opposite, dorsal side. This explains why the nectophores are late in appearing where they do on the dorsal side. Metchnikoff says that the pneumatophore has become free, in his figure 1, through the loss of one of the larval bracts. He draws attention to the beginnings of a stem; to the one-sided position of the nectophores; to the first definitive bract below them; to four palpons; and to the two (larval and first definitive) tentacles and a single gastrozooid. Evidently he was unaware of the smaller protozooid or confused it with a palpon. This is the only published account known to me of the beginnings of metamorphosis in a physonect siphonophore.

But curiously enough metamorphosing Physonects, probably of more than one species, have been figured unwittingly as adult representatives of a distinct genus "*Nectalia*". Garstang (1946, pp. 172–5) spent much time discussing "*Nectalia*" He quite correctly perceived that its long bracts were precormidial, or coronal as I prefer to call them, and homologous with the bracts of *Athorybia rosacea* and of *Melophysa melo*. But the reasons for his conclusion appear to be wrong in that he implied that these bracts would not be carried downwards with increase in number of the cormidia. The coronal (larval) bracts of Agalmids are in fact carried downwards with the first and second gastrozooids. They are "precormidial" in the earliest stages only. New bracts of this coronal type are formed for a long time after metamorphosis, but only in this restricted area, which comes to be terminal, and on the distal (oral) side of their predecessors. The later-formed bracts of this type are much longer than the first-formed ones, and gradually diverge from them somewhat in shape. But from the start they have a distal pocket of nematocysts at the end of the bracteal canal (misinterpreted by Haeckel as a medusoid subumbrella), whereas the cormidial (definitive stem) bracts in *Agalma elegans* do not.

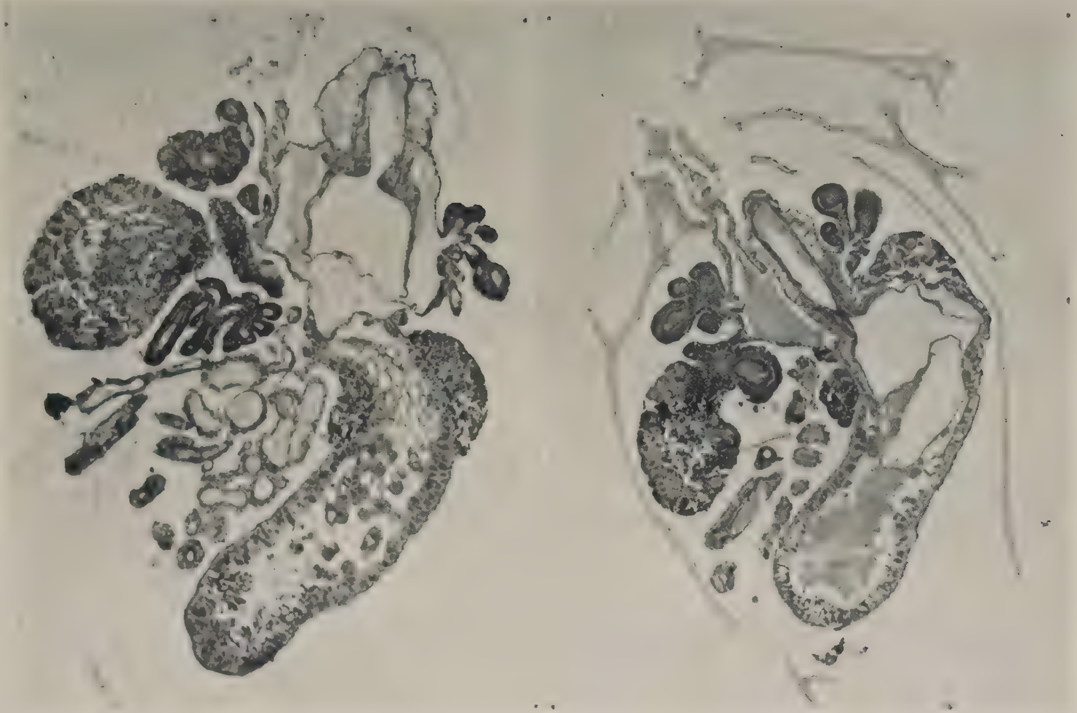


Fig. 1. Sagittal sections of two *Athorybia*-larvae of *Agalma elegans* taken with a plankton net at Villefranche. (*a*) (right) shows the bracts arising from the nectostyle, from the lower part of which are budded off the secondary gastrozooids. On the opposite side of the pneumatophore can be seen buds of the nectophores. Just below these is seen the small basigaster of the protozooid, and below this again the lower part of the pneumatosac, which at this stage is lodged inside the larval body. (*b*) A later stage. The pneumatosac is now outside the larval body. Between the latter and the second gastrozooid can be seen the larval tentacle and the budding zone of the first definitive tentacle.

Symbols used in figures throughout:

Pn.	Pneumatophore	T. larv.	Larval tentacle	Nec.	Nectostyle	Pal.	Palpon
N.	Nectophore	Gz. 2, 3.	Second and third gastrozooids	Bg.	Basigaster	Pr. Z.	Protozooid

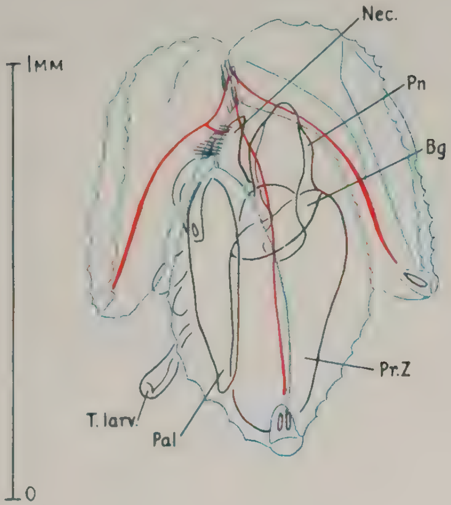


Fig. 2. An early *Athorybia*-larva of *A. elegans* showing attachment of larval bracts to the nectostyle and the first of a ring of palpons that come to surround the protozooid.

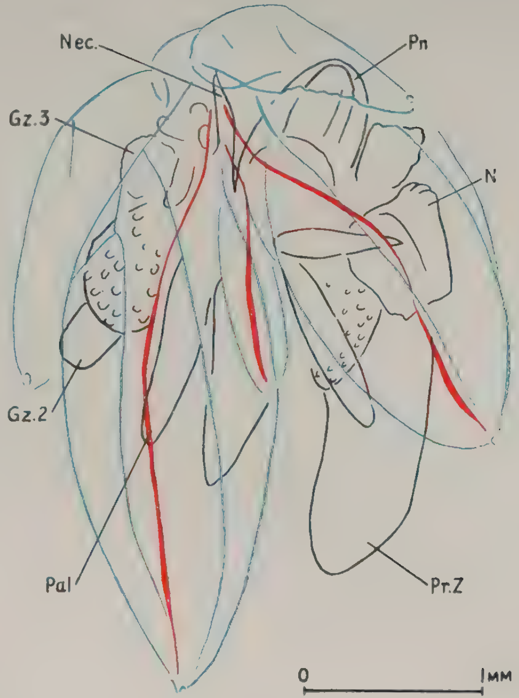


Fig. 3. The youngest larval bract still covers the pneumatophore. Palpons have increased in number, the nectophores are larger and the second gastrozooid has grown in size.

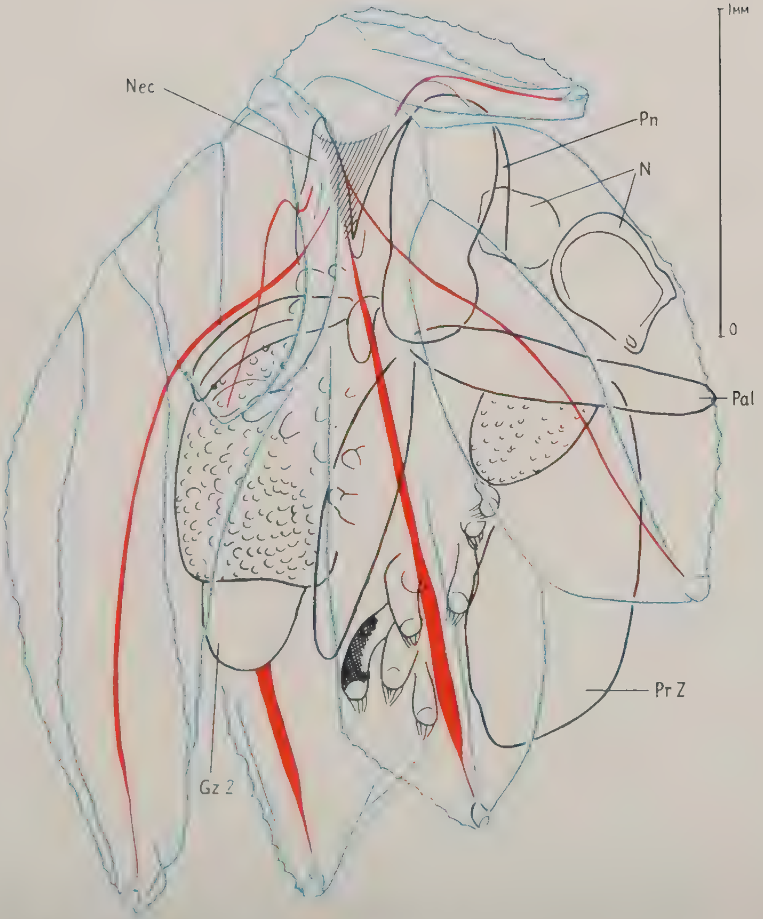
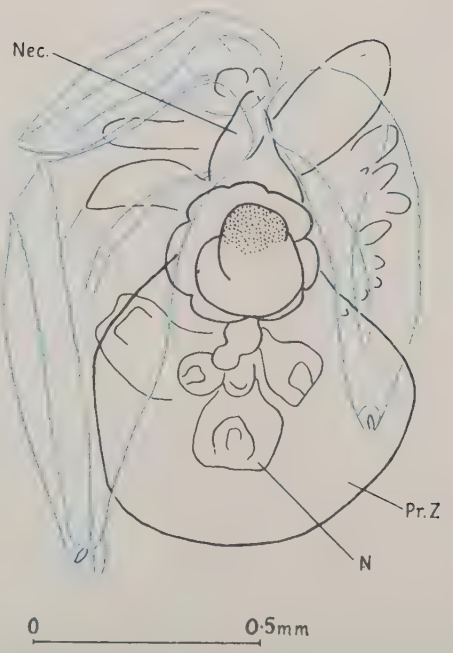

Nec
Pn
N
Pal
Pr Z
Gz 2
1MM
0

Fig. 4. The second gastrozooid is as large as the protozooid. Only one of the delicate muscularlamellae which attach the bracts to the nectostyle is indicated.


Nec.
Pr. Z
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0
0·5mm

Fig. 5. An apical view of an anaesthetized larva to show that the buds of the nectophores are attached on the side of the pneumatophore opposite to the nectostyle.

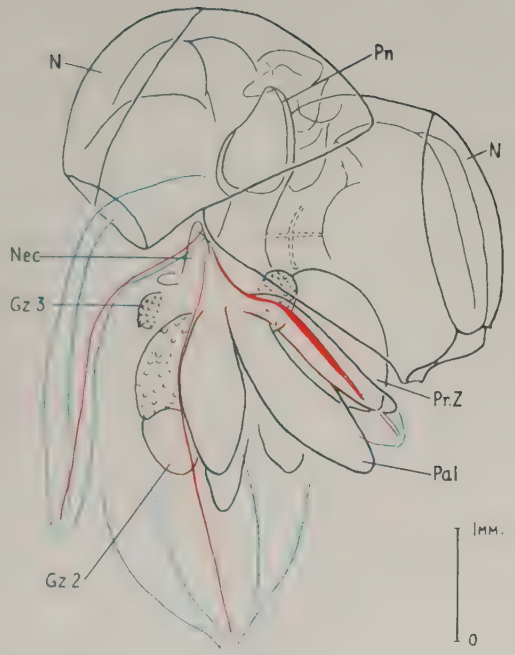

Fig. 6. An early stage in metamorphosis. That side of the upper end which carries the pneumatophore has elongated to carry the latter above the coronal bracts, and the nectophores have grown and are functional. The protozooid has taken up a latero-terminal position, leaving the second gastrozooid at the end.

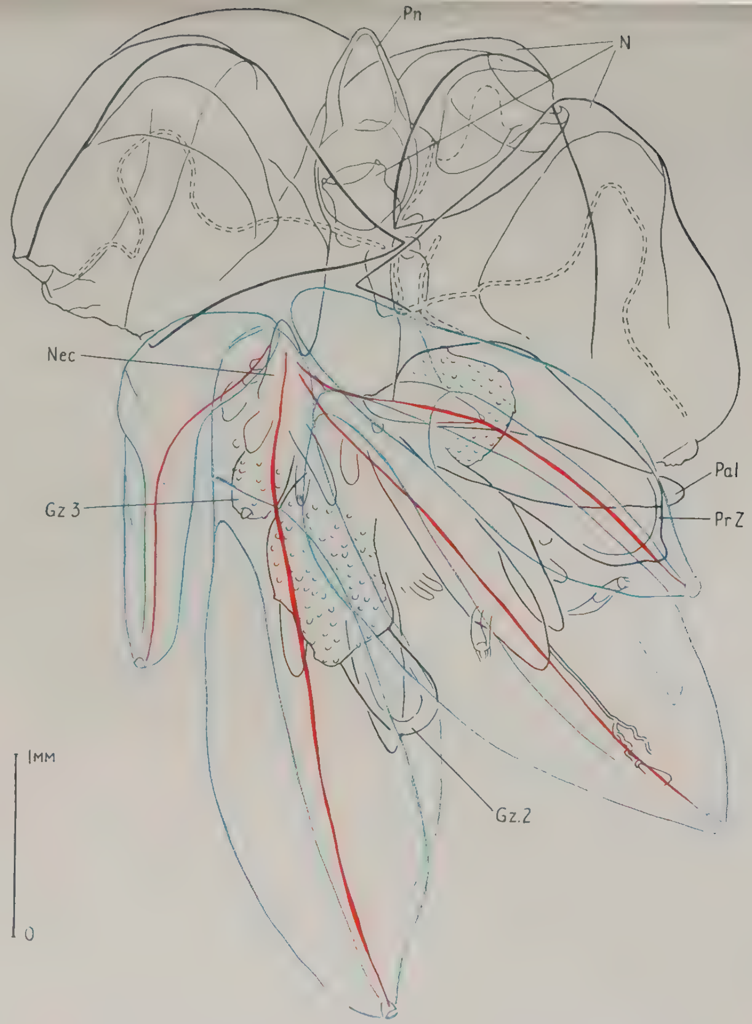

Fig. 7. The nectosome has elongated, but the siphosome has not. Note the small size of the basigaster of the protozooid compared with that of the second gastrozooid. The nectostyle can be seen clearly, still carrying the coronal series of bracts, and buds of stem appendages.

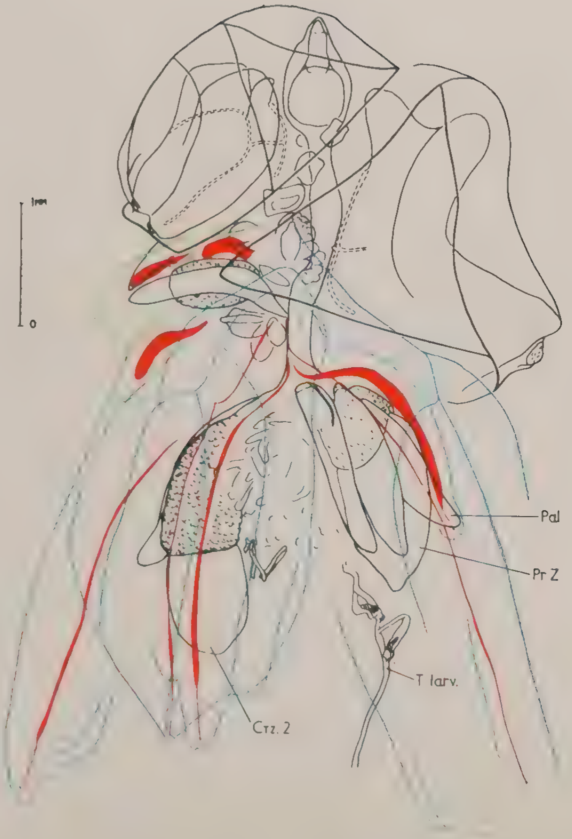

Fig. 8 The first of the definitive stem bracts coloured green can be seen on the elongating siphosome.

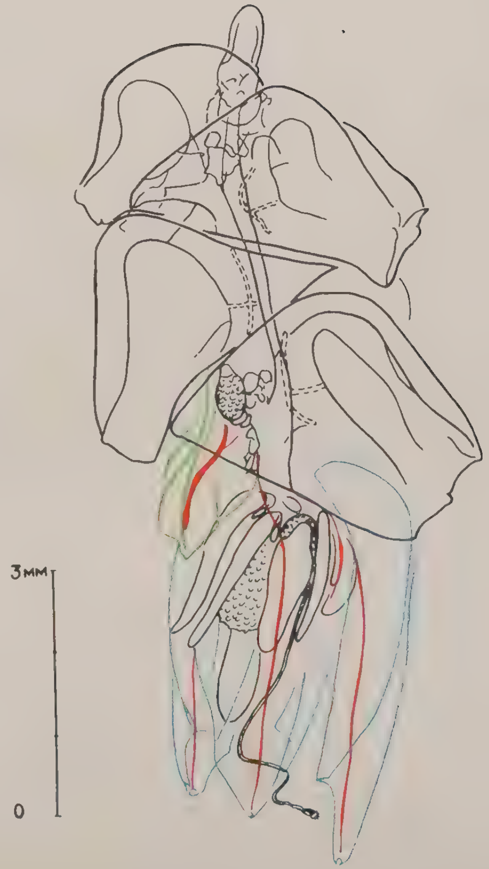

Fig. 9. The small size of the displaced protozooid is shown. The second gastrozooid now exceeds it in size. The nectostyle can still be seen opposite the pedicel of the first nectophore. Tentacles not indicated except for part of larval one.

Metamorphosis may be said to begin at the time when, the second gastrozooid being still smaller than the protozooid, and further cormidial buds having already made their appearance on the ventral side of the nectostyle (Figs. 3, 4), the stem of the future nectosome appears (Figs. 6, 7) as an elongation of that part of the oozooid that lies dorsal to the nectostyle. The nectostyle carries the larval bracts, rather like the tip of a man's umbrella with its bare ribs spread open, and also the cormidial buds. It remains at what may be called the nodal point of minimum growth, where it can be recognized at the side of the stem for some time, whilst the elongating stem of the nectosome carries the budding zone of the nectophores upwards and away from it in an aboral direction.

The second gastrozooid by now has overtaken the protozooid in size, and the adult type of tentilla on its tentacle can be seen (Fig. 8).

The upper end of the pneumatophore may have grown upwards as much as 4 mm above the nectostyle before there is a noticeable elongation of that part of the stem (siphosome) lying between the second and third gastrozooids. By the time that the nectosome, measured from tip of pneumatophore to nectostyle, is 5·5 mm in length, the siphosome, measured from nectostyle to base of first and second gastrozooids, may be 2 mm in length (Fig. 9).

An interesting point about the post-larva during this stage of metamorphosis is that the second gastrozooid comes to exceed the protozooid in size, and to assume a terminal position, leaving the smaller protozooid on the dorsal side. The protozooid too has a much smaller basigaster, which is partially divided on the outer, dorsal side. Its relatively small size can be seen in my frontispiece (1954, Fig. D. Gz. (rd)). At that time I had not studied the earlier developmental stages, which I have since collected in abundance, and confused the protozooid with the first definitive gastrozooid.

This side tracking of the protozooid is still more pronounced in *Nanomia bijuga*, where it becomes vestigial. The significance of this seems to be that it marks a new line of evolutionary experiment, an escape from the old line of specialization. This is all the more probable since the primitive type of tentacle found on the protozooid is replaced by a much more highly evolved type in the new series of gastrozooids. This " adult " trifid type of cnidosac demands more and bigger nematocysts. The basigasters of the secondary series of gastrozooids which supply the nematocysts are correspondingly better developed.

REFERENCES

FEWKES, J. W. (1881), Studies of the jelly-fishes of Narragansett Bay. *Bull., Mus. Comp. Zool., Harvard Coll.*, **8** (8), 141–182.

FEWKES, J. W. (1885), Studies from the Newport Zoological Laboratory. XV. On the development of *Agalma. Bull., Mus. Comp. Zool., Harvard Coll.*, **11** (11), 239– 275.

GARSTANG, W. (1946), The morphology and relations of the Siphonophora. *Quart. J. Micr. Sci.*, **87** (2), 103–193.

HAECKEL, E. (1869), Zur Entwickelungsgeschichte der Siphonophoren. *Natuurk. Verh. Prov. Utrechtsch, Genoots*, (1), **6**, 1–120.

METSCHNIKOFF, E. (1874), Studien über die Entwickelung der Medusen und Siphonophoren. *Z. Wiss. Zool.*, **24**, 15–83.

TOTTON, A. K. (1954), Siphonophora of the Indian Ocean together with systematic and biological notes from other oceans. *Discovery Repts.*, **27**, 1–162.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 242-249.

Observations on the biology of *Microsetella norvegica* *

By Charles J. Fish
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Summary—*Microsetella norvegica* is one of two microcopepod species which appear significant in the natural economy of certain western Atlantic boreal waters. During the winter months it extends its range southward at least as far as the latitude of Chesapeake Bay. North of Cape Cod in the Gulf of Maine region it is widespread with a tendency to form concentrations of limited area.

Propagation in 1932 began in March in the outer area between Georges Bank and Cape Cod and gradually expanded as the season progressed until it reached a peak in the Gulf along a band seaward of the 100 metre curve from Casco Bay to the Bay of Fundy.

There is evidence of three and possibly four generations between March and September. As in other endemic pelagic species there was a progressive delay to the eastward in the time of spawning, but unlike most of these *Microsetella* was found propagating successfully at low summer temperatures, averaging 11°–13·5° C, in the turbulent eastern (Frenchman's Bay) area.

INTRODUCTION

There has been increasing recognition of the importance of adult and larval microcopepods in the natural economy of both coastal and open ocean waters. Because of their small size and frequent preference for subsurface levels they cannot be representatively sampled with nets of the mesh most frequently used for zooplankton, and, consequently, are commonly much more important members of the pelagic population than published records indicate.

One member of this group, *Oithona similis* Claus, which Wilson (1941) has concluded to be the most widely distributed and numerous of all copepods, is also one of the most prolific in western Atlantic boreal coastal waters where its young provide an abundant source of food for larval plankton feeders in midsummer (Fish, 1936 c).

Relatively little attention has so far been accorded *Microsetella norvegica* Boeck, a second and even smaller (0·3–0·5 mm) microcopepod species, also endemic in boreal coastal waters. Although widespread, it has not been reported to be particularly abundant in north European coastal areas (Ruud, 1929; Störmer, 1929; Wiborg, 1954) or south of Cape Cod in the western Atlantic (Fish, 1925; Deevey, 1952).

Table I

Mean numbers of Microsetella norvegica *in Frenchman's Bay. Number per cubic metre. Upper 50 metres*

1930	*Adults-Copepodites*	*Nauplii*
July 10	208,360	404,720
July 18	293,467	195,567
August 1	248,850	169,523
August 7	152,820	92,850
August 14	295,460	93,600

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* Narragansett Marine Laboratory Contribution No. 11.

However in certain localities north of Cape Cod it is at times very numerous. For example, in Frenchman's Bay it was found by the author to be the dominant species during two months of weekly observations in July and August 1930, when adults and young often comprised over 90% by number of the total zooplankton population. Again in 1931 in the same region 17,907 adults per cubic metre were taken in the upper 50 metres near Monhegan Island on August 21.

To determine its importance elsewhere in the Gulf of Maine and Bay of Fundy, an analysis has been made of collections obtained between July 28, 1931, and September 29, 1932. The area covered, location of stations and methods have been described in a previous report (Fish, 1936 A).

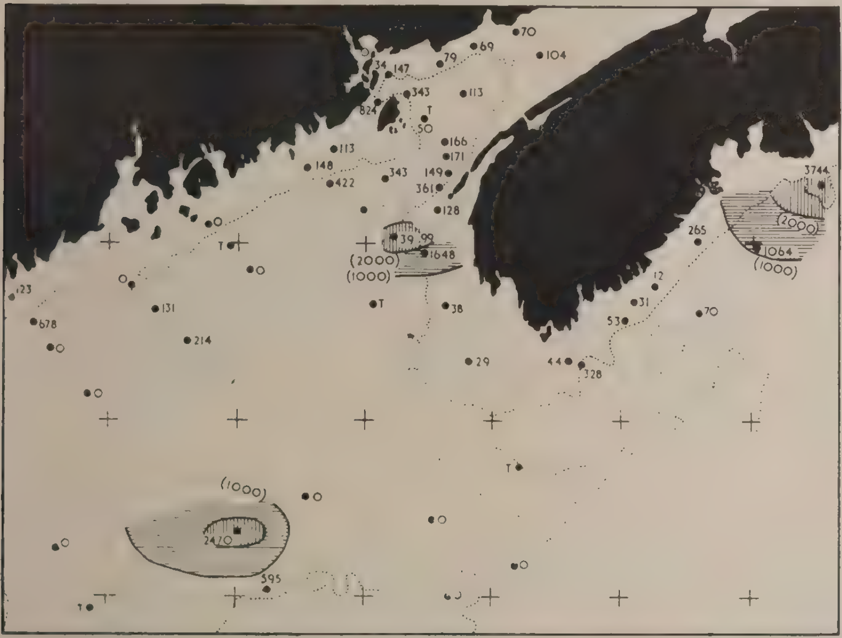

Fig. 1. Distribution of adult *Microsetella norvegica* in April 1932. Number per minute of towing

REGIONAL DISTRIBUTION OF THE ADULT STOCK*

In the western Atlantic *M. norvegica* ranges from Arctic waters (76° 02′ N, JESPERSEN, 1923) at least as far south as Chesapeake Bay where it was found by WILSON (1932) in December 1920 and January 1921. At Woods Hole it appeared in late March and early April 1923 (FISH, 1925), in Narragansett Bay in March 1906 (SHARPE, 1910) and in Block Island Sound in October and December 1949 (DEEVEY, 1952). These records indicate that, like most boreo-arctic plankton animals, *M. norvegica* extends its range southward along the coast during the winter months.

North of Cape Cod it is widespread in the Gulf of Maine and Bay of Fundy, with a tendency to form local concentrations of limited area (Fig. 1). When first observed in April 1932, the numbers were everywhere relatively sparse except in three widely separated localities where more than 1,000 per minute were taken in oblique hauls with half metre nets of number 10 mesh. Two of these were near the Nova Scotian coast, one approximately 25 miles east of Briar Island (3,999 per minute) and the other off Halifax (3,744 per minute). A third (2,470 per minute) was located off the inner margin of Georges Bank between the middle and western channels.

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* Mature individuals and late copepodite stages have been combined in the counts.

Varying numbers, usually small, were taken at all stations east of Mt. Desert in the Gulf, the Bay of Fundy, and along the west and south coasts of Nova Scotia. West of Mt. Desert, *Microsetella* appeared at but five of ten stations in the inner Gulf, and in the outer Gulf at but four of nine stations. The two eastern centres of abundance coincided with similar local concentrations of *O. similis* (FISH, 1936 C), the numbers of the two species off Halifax being approximately the same. The richest hauls of both species in the inner Gulf, at this time, were also obtained at the same location, St. 24A, seaward of the 100 metre contour off Casco Bay.

With observations restricted to the inner Gulf and Bay during the balance of the season, it was not possible to determine the duration of the three *Microsetella* concentrations observed in April. The distribution in succeeding months reveals a progressive shoreward movement of the eastern and western adult-copepodite stocks and gradual expansion to a seasonal peak everywhere in the inner Gulf seaward of the 100 metre contour (Fig. 2). Here the members ranged from 1,360 to 5,662 per cubic metre in August.

Contrasted with 1932, records for August 1931 show much smaller numbers at all comparable stations, although the local swarm near Monhegan Island (p. 243) yielded the highest counts of the two seasons. By September the numbers in the Bay of Fundy had declined greatly both in 1931 (188 per cubic metre) and in 1932 (179 per cubic metre).

PRODUCTION AND DISPERSAL

There are few available data on the biology of *Microsetella norvegica*, in fact the developmental stages, some of which are shown in Fig. 3, have not yet been described to the author's knowledge. The seasonal occurrence of adults south of Cape Cod would suggest that, like *Pseudocalanus*, spawning may begin at the southern portion of its range as early as November or December. It is not known, however, whether propagation continues offshore in deeper water after the species disappears from neritic areas south of the Cape with rising spring temperatures.

Distribution of eggs and larvae in 1932

By mid-April propagation in the Gulf was most advanced in the outer part of the western basin between Georges Bank and Cape Cod. Here late nauplius stages up to 1,544 per minute were found at two stations. Farther east in the outer Gulf spawning was still taking place and egg sacs up to 926 per minute were found coinciding with the local concentration of adults. Smaller numbers of early nauplii (309 per minute) appeared at one station in this region. Still farther east along the outer Nova Scotian coast neither eggs nor larvae were found. In the inner Gulf spawning had just begun in the eastern basin (up to 1,666 egg sacs per minute) and small numbers of eggs were found extending into the Bay of Fundy. Only one station (St. 29) west of Petit Manan yielded eggs at this time, and no larvae appeared anywhere in the inner Gulf or Bay.

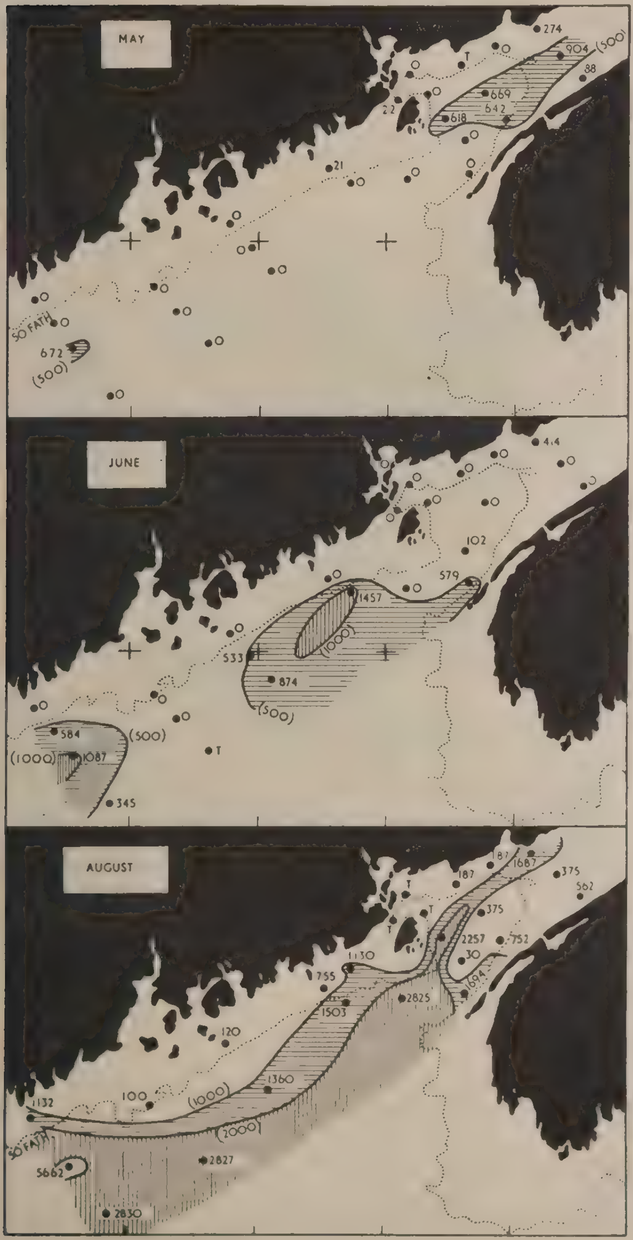
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Fig. 2. Distribution of adult *Microsetella norvegica* in 1932. May–June: number per minute of towing. August: number per cubic metre

In late May propagation extended to the western part of the inner Gulf where local patches were found off Casco Bay and Mt. Desert. East of Mt. Desert, egg sacs were taken only along the Nova Scotian side of the Bay of Fundy.

The June distribution would suggest offshore production in the eastern and western basins of the Gulf. Eggs were restricted largely to the two outer stations of the most western section and along the course of the drift into the Bay.

Propagation in the inner Gulf reached its peak in July and early August. By mid-August the greater part of the stock was in late nauplius (Fig. 4) and copepodite stages, the largest hauls (plus 2,000 per cubic metre) occurring along a band seaward of the 100 metre curve and extending from Casco Bay to the Bay of Fundy. Early nauplii, presumably the product of the eastern area, appeared in small numbers, restricted almost entirely to the eastern part of the Gulf (Fig. 4). Eggs were widely scattered in small numbers in the Bay of Fundy, particularly in the entering drift and at a few stations farther west in the Gulf.

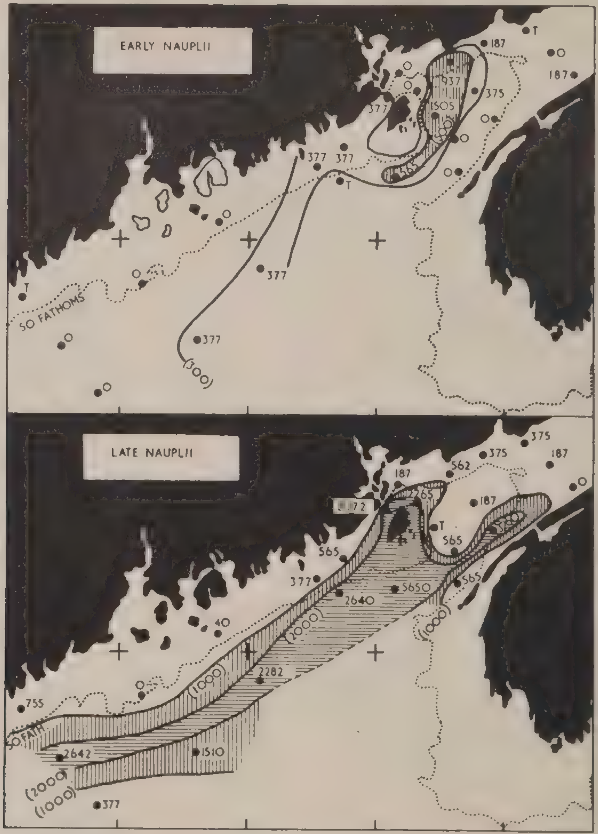
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Fig. 4. Late nauplii of *Microsetella norvegica*, presumably the western stock, and early nauplii of the eastern stock in August 1932. Number per cubic metre

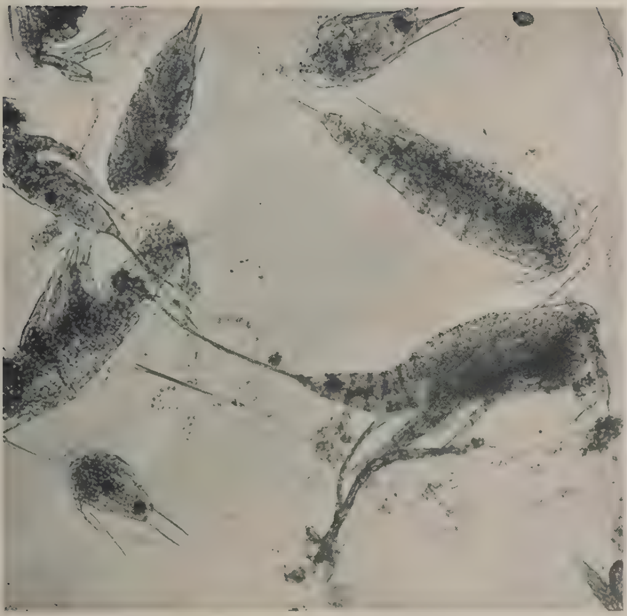

Fig. 3. Developmental stages of *Microsetella norvegica* taken in Frenchman's Bay on August 1, 1930

By September few eggs and young remained in the Bay, the largest number of nauplii, 374 per cubic metre, being taken in New Brunswick waters off Point Lipreau.

Table II

Mean numbers of adults and egg sacs of Microsetella norvegica *in successive months. April–June: number per minute. August–September: number per cubic metre. - - - : no observations*

Year	*Month*	*Gulf of Maine*		*Bay of Fundy*	
		Adult	*Egg sac*	*Adult*	*Egg sac*
1932	April	150	9	104	38
	May	45	243	328	177
	June	425	109	103	321
	August	1264	170	776	250
	September	—	—	179	37
1931	August	423	189	—	—
	September	—	18	188	T

DISCUSSION AND CONCLUSIONS

Annual cycle

Possibly because of its very unequal distribution during the early season, developmental stages of *Microsetella* were not taken in sufficient numbers to permit tracing with certainty successive generations in different areas until August.

Considering the region as a whole, it appears probable that, like *Oithona*, there are at least three and possibly four generations of the stock spawning in late March and reaching late nauplius stages in mid-April. A second breeding period is indicated by an increase in egg sacs in the Gulf in late May (Table II) followed by an increase of copepodite-adults in June. The abundance of late nauplius-copepodite stages combined with relatively few egg sacs in August (Table III) suggests a maturing of the second generation and the appearance of a third crop of eggs in July. Egg sacs in the Bay of Fundy on September 15–16 may represent a fourth relatively unimportant generation. There would thus appear to be propagation periods in March, May, July and possibly September, with a cycle of approximately two months.

Table III

Mean numbers (per cubic metre) of Microsetella norvegica *in different areas in* 1931 *and* 1932

	Total Gulf		*Western Area*		*Central Area*		*Bay of Fundy*	
	1931	1932	1931	1932	1931	1932	1931	1932
	Aug. 21–26	Aug. 8–15	Aug. 21–25	Aug. 11–14	Aug. 26	Aug. 8–15	Sept. 4–5	Sept. 15–16
Egg sac	376	103	489	126	93	94	T	37
Early nauplius	162	188	227	94	—	188	112	61
Late nauplius	698	1531	920	1006	141	958	225	51
Copepodite-Adult	2922	1840	3998	2336	234	1001	150	211

Regarding regional production, *Microsetella norvegica* appears first as an offshore species which later penetrates and propagates in the inner Gulf some time after augmentation has taken place in the region of the outer banks. The brood in the vicinity of the south channel had attained late nauplius stages by mid-April in 1932, when eggs but no larvae were found in the eastern basin. No evidence of propagation was found farther east off Halifax at this time, or in the inner Gulf west of Mt. Desert where the first evidence of local production was found in late May and June. As in the outer region, and corresponding to *Calanus finmarchicus* (FISH, 1936 A), *Pseudocalanus minutus* (FISH, 1936 B) and *Oithona similis* (FISH, 1936 C), a progressive delay to the eastward in the time of spawning was evident in the inner coastal area after the species had become established there in 1932. This is indicated in Fig. 4 showing early nauplii limited to the eastern Gulf at a time when late nauplii, presumably the western crop, dominated everywhere. By September, propagation had largely ceased in the Gulf, both in 1931 and 1932 (Table II).

Although the progressive delay to the eastward in the time of spawning, and the relatively small numbers of adults and larvae in the New Brunswick region of the Bay of Fundy (Figs. 2 and 4) indicate that *Microsetella* responds in a general way to the limiting factor of low temperature, in a manner characteristic of the boreal zooplankton population, there is evidence that it can reproduce at somewhat lower temperatures than *Calanus* and *Pseudocalanus*. In Frenchman's Bay in 1930 (Table I) *M. norvegica* propagated successfully in large numbers during July and August at surface temperatures averaging from 11°–13·5° C. and was the only pelagic copepod (with the exception of *Temora longicornis*) found developing in those waters. An abundant population of offshore species dominated by *Calanus* and *Pseudocalanus* (adults and late copepodite stages) was present in the lower levels of Frenchman's Bay throughout the summer of 1930, but their eggs and larvae rarely appeared in the collections.

Table IV

Relative abundance of adults of Oithona similis *and* Microsetella norvegica *in the Gulf of Maine and Bay of Fundy in* 1931 *and* 1932. *April–June: mean numbers per minute. August–September: mean numbers per cubic metre.* - - -: *no observations*

1932	*Gulf of Maine*		*Bay of Fundy*	
	O. similis	*M. norvegica*	*O. similis*	*M. norvegica*
April	1380	150	212	78
May	3672	45	983	246
June	4534	425	1858	77
August	3735	1635	3120	770
September	—	—	332	179
1931				
August	3550	423	—	—
September	—	—	94	188

It would appear, therefore, that although *Microsetella* and its nauplii ordinarily provide a less abundant supply of food for summer larval plankton feeders in the Gulf of Maine and Bay of Fundy than *Oithona* they do appreciably supplement the latter stock in those waters and seem to be of particular significance in areas like Frenchman's Bay and the adjacent turbulent coastal region eastward from Mt. Desert where low surface temperatures prevent successful summer propagation of the more dominant Gulf zooplankton species.

REFERENCES

DEEVEY, G. B. (1952), Quantity and composition of the zooplankton of Block Island Sound, 1949. *Bull. Bing. Oceanogr. Coll.*, **13,** Art. 3, 120–164.

FISH, C. J. (1925), Seasonal distribution of the plankton of the Woods Hole Region. *Bull. U.S. Bur. Fish.*, **41,** 91–179.

FISH, C. J. (1936 A), The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, **70,** 118–141.

FISH, C. J. (1936 B), The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Ibid.*, **70,** 193–216.

FISH, C. J. (1936 C), The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Ibid.*, **71,** 168–187.

JESPERSEN, P. (1923), Dr. Thorild Wulff's plankton collections in the waters west of Greenland. *Den II. Thule ekspedition til Gronlands nord Kyst.*, 1916–18, No. 4.

RUUD, J. T. (1929), On the biology of copepods off Möre, 1925–1927. *Rapp. et Proces.-Verb., Cons. Perm. Int. Explor. Mer*, **56,** 1–84.

SHARPE, R. W. (1910), Notes on the marine Copepoda and Cladocera of Woods Hole and adjacent regions, including a synopsis of the genera of the Harpacticoida. *Proc. U.S. Nat. Mus.*, **38,** 405–436.

STÖRMER, L. (1929), Copepods from the *Michael Sars* Expedition, 1924. *Rapp. et Proces-Verb., Cons. Perm. Int. Explor. Mer*, **56,** 1–57.

WIBORG, K. F. (1954), Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. *Fiskeridirektoratets Skr.*, **11,** Art. 1, 5–246.

WILSON, C. B. (1932), The copepod crustaceans of Chesapeake Bay. *Proc. U.S. Nat. Mus.*, **80,** Art. 15, 1–54.

WILSON, C. B. (1942), The copepods of the plankton gathered during the last cruise of the *Carnegie*. *Carnegie Inst. Wash., Pub.* 536, 1–237.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 250-256.

The production of *Liza ramada* (Risso) in Lake Mariut, Egypt

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Summary—The production of the grey mullet *Liza ramada* in Lake Mariut, Egypt, is followed from its introduction in 1920 until 1935, special attention being paid to the years 1928–31 and 1933, when age censuses were available.

After an initial build-up to a steady state between 1923 and 1926, it is thought that a decline set in about 1927–8 due to a lowering of the lake-level, and that this ended in lower levels of the population from 1930 to 1933 and a further fall in 1934 and 1935. The decline in numbers estimated in the O group catch represented a heavy mortality in the first year, and it is thought that this occurred very soon after the fry were introduced into the lake, as the rate of growth of fish caught in their first year in the lake showed no fall, but a slight increase between 1928 and 1933.

On the delta coast of Egypt there are several large and extremely shallow lakes usually connected with the sea during the whole or a part of the year by shallow channels. They are of great fertility, 60–270 kgm per hectare compared with 100 to 400 kgm per hectare for cultivated carp ponds in Germany, and 5 to 250 kgm per hectare for cattle on grassland (Mortimer, 1954). Among the species that go to make up the yield are those of the genus *Tilapia* which can give over 9,000 kgm per hectare in the fertilized ponds of the Belgian Congo (Mortimer, 1954) and the grey mullets, a species of which constitutes 50–60% of a yield of 1,500–4,000 kgm per hectare for the brackish ponds in the New Territory of Hong Kong (Bromhall, 1954). It is one of the most important species of this latter group, *Liza ramada* (Risso) formerly called *Mugil capito* Cuv. and known locally as the " Tobar " which is the subject of this contribution.

The habit of the Tobar is to enter the lakes from the sea in great numbers between January and April. During this time it will be found to increase in modal size from 16 to 20 cm during the course of the run. The fry which enter the lakes already possess scales, the gut is short and simple and both animal and vegetable plankton is eaten. Subsequent growth is rapid and the intestine becomes lengthened and convoluted as the fish changes its feeding habits to that of a mainly vegetarian browser.

The length range of the commercially caught population is from 14–30 cm long and the average size, which also happens to be near that at which both sexes may first be commonly found mature, can be taken as 20 cm. Growth to the end of the first year (" O group ") appears to vary a good deal and fish may be from 14–20 cm, indeed in exceptional circumstances in fresh water ponds 28 cm has been reached in this time. In the second year (" I group ") length can increase by from 1 to 6 cm, and in the third (" II group ") 1 or 2 cm. Generally, however, there appears to be little growth after maturity has been reached.

When in October and November sexually mature fish leave for the sea in large shoals, most of these are at the end of their second year. Spawning must take place in the immediate coastal belt, as no record is known of any individual of this species being caught in the trawl, or by any other method of fishing employed outside the littoral zone. Although I was fortunate enough to find and describe the planktonic egg from a population introduced into Lake Quarun (WIMPENNY, 1936), none has been found in the water of the coastal belt either near Lake Mariut or anywhere else in the world, and the location of the actual spawning grounds, bearing the number of eggs that must necessarily be present to account for the origin of the huge runs of young fish into fresh water, remains a mystery.

There is, therefore, a gap in our knowledge of the life cycle of this species between the departure of the spawning shoals and the arrival of swarms of small scaled individuals in the out-flowing fresh water at the beginning of January.

Lake Mariut during the period to which this account refers was an area of approximately 59,000 acres of water rarely more than 50 cm deep and situated behind the town of Alexandria. The Department of Irrigation maintained it around a level of 3 metres below sea-level (rather above this in the early part of the period, rather below later), and it acted as a drainage reservoir for the farm lands of the north-west part of the Nile delta. The drain water reaches the lake chiefly through a large channel called the Omoom drain. A channel at sea-level runs from the sea to the lake-side at a place called Mex. Here powerful pumps force the water from a canal on the lake-side up into the sea canal. It was usual for these pumps to work from August to April, as during the rest of the year the evaporative power of the sun, estimated to have been 750,000 to 1,000,000 tons per day, was considered sufficient to keep the lake at the required level.

The effect of these arrangements was that there was no contact between sea and lake when the pumps were not working, but for the rest of the time the water flowed with considerable velocity from the lake to the sea. The sea water never flowed into, nor was it on a level with the lake; thus the penetration of marine animals was obstructed. In these circumstances spawning shoals of Tobar found it easy to leave the lake in the spawning season, but the fry, attracted to the outflow of fresh water in the Mex channel, were prevented from passing in through the pumps, and gathered against the walls of the channel with their heads facing upstream as near the pumps as possible. There they collected in great numbers, and until 1920 this obstacle to their progress stopped other than stray individual Tobar, that had wandered into the lake by the inland drains, from populating the lake.

In 1920 the Director of Fisheries Research of that day, Mr. PAGET, organized a service of transplantation which consisted in sweeping up the fry from alongside the walls of the marine canal by long-handled nets having a mosquito netting bag and a rectangular head. The fry thus caught were carried to the lake-side of the pumps in buckets, and poured into boats with perforated zinc removable sides. When the boats were sufficiently charged with fry, they were towed some distance out into the lake and the fry released. The bags of the nets were marked so that a record of the number of fry could be kept. This introduction, made at a cost of a few hundreds of pounds annually, resulted in a fishery for two species of grey mullet running into tens of thousands each year.

For the fifteen years 1920–35 there are available (Egypt, Government Press, 1922-26) (a) statistics concerning the weights and values of the different species of fish collected at the landing places on Lake Mariut; (b) the record of numbers of fry introduced; (c) information on the number of fishing boats at work (from the licensing system) and (d) particulars relating to the water level and supply (from the Department of Irrigation). In addition to this, for the years 1928–31 and 1933, there are some observations on the age, length and weight composition from samples of the commercial catch. The age, length and weight data for 1930, 1931 and 1933 are published here for the first time. On this basis therefore and, as far as the data permits, it is proposed to follow the annual production of Tobar in Lake Mariut for the first fifteen years after its introduction, and to examine the changes revealed, paying special attention to the years 1928–31 and 1933.

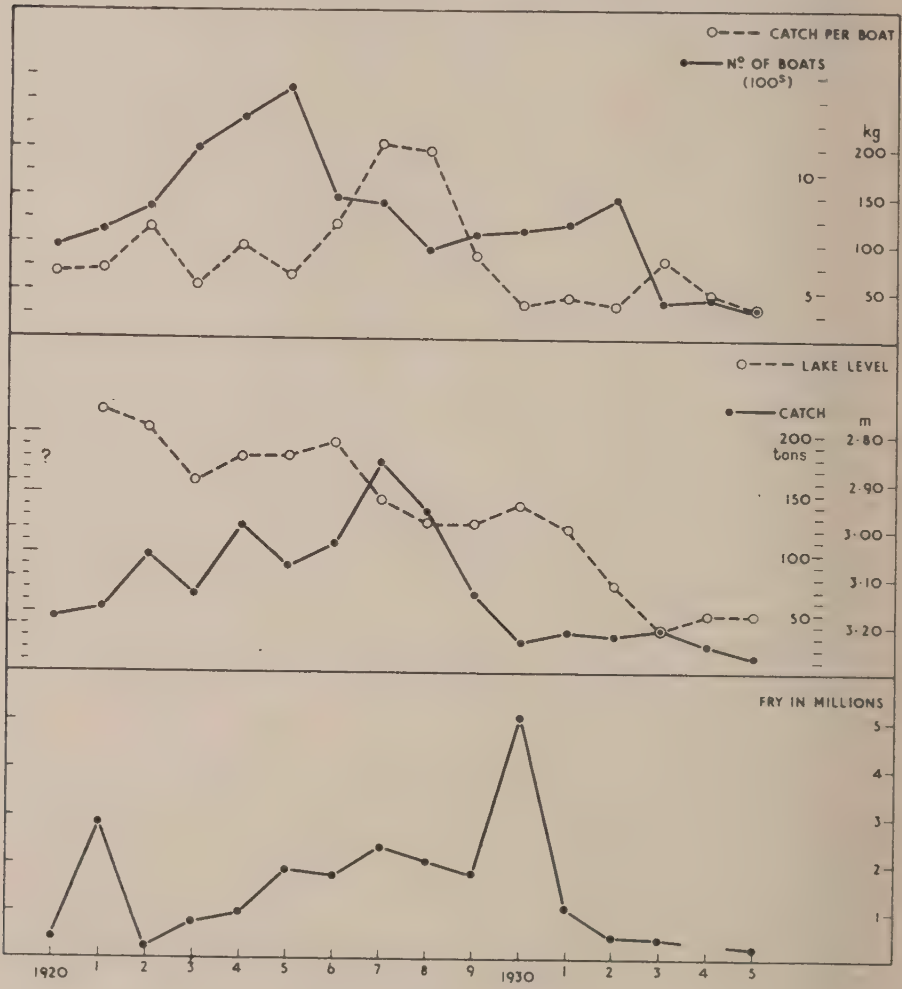

Fig. 1

Relation of fry to catch

The relation of fry introduced each year to the corresponding catch is shown in Fig. 1. In a general way the fry introductions built up parallel to the catch until 1927, and thereafter fell away to lower levels in the thirties. There are, however, two years, 1921 and 1930 in which the unusually high values of 28·6 and 51·1 millions are associated with unexpectedly low catches. Inspection of the graph gives the impression that catch rises roughly in proportion to fry introduced up to about 25 million, but that two higher values than this correspond to lower catches, perhaps due to high mortality from more acute competition among the more numerous fry.

A correspondence between the catch and the number of fry introduced is not difficult to imagine, and it seems reasonable to suppose that it could happen in two ways. First of all it is to be noted that a substantial yield of catchable fish, 47 tons per 4·7 million fry, occurred in the year of first introduction, and it is reported that a number of these left the lake to spawn in the first year. The introduction of fry in any one year may therefore be expected to have a substantial effect on the yield. Secondly, as a fair proportion of the fish spawn in their first year, a successful year-group may be indicated by a good catch and the origin of a successful spawning. This would mean there might be a correspondence between the catch in one year and the number of fry that appeared in the succeeding year.

In fact when the catch and contemporary fry were correlated, a low but positive correlation of little significance was obtained. It is not without interest, in view of the preceding remarks, to report that for the relation between the catch and the fry introduced a year later the correlation was somewhat higher.

From age, length, and weight samples given in Table II, and in the Egyptian Fisheries Reports for 1920, 1928–31, and 1933, estimates of the numbers of O group fish caught in 1920, 1928–31 and 1933 have been devised and shown in Table I. The numbers have been obtained by dividing the estimated mean individual weight into the weight of the Tobar landings for the periods August–December of the appropriate years. These estimates may be compared with the corresponding fry introductions.

It will be seen that in 1920 nearly a million fish of commercial size were taken out of the lake within nine months of introducing about 4·7 millions. This is to say that it needed rather less than five fry to produce a marketable O group fish. By 1928 it took 50 fry to do this, and the O group caught had fallen to about 400,000—a fall which continued steadily until 1933. The number of fry necessary to produce one commercial O group fish increased until in 1930 it was nearly 800, but thereafter it went back to 269 in 1931 and 132 in 1933. These observations suggest that the conditions for survival must have deteriorated throughout the period. Against this it must be remarked that the estimated proportions of O group fish in the August–December catch, where they may form part of the spawning shoals, fell from 42% to 17% between 1928 and 1935, and it may be that more O group stayed on in the lake to become 1 group in this period. Nevertheless, from 1929 to 1931, when the percentage of O group was steady, it appears that the O group numbers continued to fall, and survival conditions were still getting worse.

Catch, Effort and Lake-level

The catch (Fig. 1) may be broken up into five periods, three of adjustment and change and two in which some stability is indicated. These are, first a period of increase from 1920 to 1923, during which the fry introductions built up the population, followed from 1923 to 1926 by a period of stability during which the catch fluctuated around a level of rather under a 100 tons. Then in 1927 there was a rise immediately succeeded by a sharp fall through 1928 and 1929 to 1930. From 1930 to

1933 the catch stabilized again at around 30 tons a year, and finally in 1934 and 1935 there were indications that a decline had set in once more.

The catch per boat also shown in Fig. 1 corresponds to the catch, and indicates that the latter is also a reasonable measure of the stock density in the lake. Considering the catch as a measure of the stock, we may therefore try to account for the catch changes just mentioned as stock changes, finding it profitable to examine these in relation to the annual mean water levels shown in Fig. 1. The water levels of such a shallow lake as Mariut must be considered as of very great importance in deciding the actual size of the habitat. The period of increase to 1923, due to fry introduction, followed by the stability or slight increase to 1926, were years in which the lake level oscillated between —2·75 and —2·90 m. In 1927, however, there was a sudden descent of 12 cm in this level, and in 1928 and 1929 of another 5, bringing the lake to —2·99 m. It is thought that this lowering of the lake made the fish more vulnerable to capture in 1927, and so explained the great increase in availability of the fishable stock. By 1928 the effect had begun to wear off, and the Annual Fishery Report for that year recording a failure of the whole fishery of the lake says, " This failure has not been confined to one or two particular species but has been one of the organic production of the lake itself. The usual rich growth of *Ruppia maritima* and floating algae was very much diminished and in some parts and at some times absent." The lake level returned to —2·94 again in 1930, but thereafter fell sharply away again to a new low record of —3·21m in 1933 and remained at —3·18m for the last two years.

The evidence on lake level, therefore, looks as if the fish stock had to make some new adjustments to its environment—a critical lowering of the lake level which appears to have begun around —2·94 or —2·95.

Age, growth and maturity

Samples taken from the lake at or around the spawning season in 1928–1931 and in 1933 are given in Table II. Length measurements were made to the centimetre below, and 0·5 cm added to allow for the distribution of length within the centimetre. Age was determined by scale readings, it having been proved by direct observations in ponds that a ring is laid down in the first scaled winter. The weights, direct in the case of the 1933 sample, were derived from the lengths in the remaining samples, using an age-length relation taken from samples of this species collected from Lake Mariut and near the entrance to Lake Menzala in November 1931.

The numbers at the different ages show that there are few that have been in the lake three winters or more (III+ group), and that the majority of the fish that are leaving or preparing to leave the lake to spawn have been therein for one winter after their introduction, and are on the eve of their second. This group has increased its proportion by weight during the period from 45 to nearly 60%, whilst that of the fish of the O group that are not quite one year old has declined from 42 to 17%. This relative decline of the O group in the spawning and pre-spawning shoals, seems most likely to be due to successively smaller O group recruitment enhancing the importance of the I group, which each represent an O group of superior strength in the previous year. The estimates of the numerical strength of the O group given in Table I support this suggestion; but it would be unwise to take these estimates too exactly, in view of the many errors involved when using such small samples as are available to me.

Another possible alternative or supplementary cause of this change might be a deferment of maturity of O group fish resulting from the increasingly adverse conditions in the lake.

With regard to growth there is also the appearance of a change in my samples between 1928 and 1933. For all ages the trend is upwards (Table II).

The continued diminution in the numbers of O group coming into the catch between 1928 and 1933 is difficult to reconcile with the apparent stability of the stock from 1930 to 1935, and it may be that this has been achieved by a deferment of maturity causing more of the O group to stay in the lake and away from the spawning shoals until they become I group, and by an increase in the growth rate. The observations however are quite insufficient to make this any more than a reasonable conjecture.

The Incidence of Mortality

The decline in the landings and almost certainly of the whole stock of *L. ramada* in Lake Mariut does not appear to have been directly attributable to changes in the supply of fry, for, as we have seen, four million fry at the commencement of the period is estimated to have produced about a million O group fish and in 1933 only a little over thirty thousand. Indeed we have seen that there is some indication that the strength of the stock in the lake may have influenced the supply of fry.

Undoubtedly the shrinking habitat of the lake caused by successive reductions in its level has been the cause of the big and successive reductions of numbers indicated by the estimates of O group fish shown in Table I. We then come to the question at what period in the life of the O group fishes is this reduction in numbers brought about.

On the observations here available I am inclined to think that the mortality takes place very early in the period. If there were a mortality acting slowly over the whole first year's life, such, for instance, as overcrowding on a ground where the food supply was not adequate for the whole population, there would be a corresponding effect on the growth-rate which has not been observed. In these circumstances I believe that an early mortality, perhaps of a catastrophic kind, occurs very soon after or possibly during the actual introduction. It must be remembered that the little mullet on first introduction has a short gut and is able to eat plankton animals, but that later it develops a long and much convoluted intestine and becomes a vegetable and detritus browser. This change-over takes place at a very early age, and would produce a condition when a food shortage caused by a shrinkage of the available shallow water habitats due to a reduction of the lake-level might be critical, and cause an immediate thinning out of stock sufficient to explain the successive reduction in O group strength.

If this is so, it would mean that each year the lake accepted a certain number of recruits corresponding to the lake level. After this acceptance was over, there appears to have been enough food for the survivors to make normal growth. Indeed, as we see in Table II, there are indications that growth has been rather better as the lake level has fallen.

The mechanism of this sort of mortality is of the greatest interest in the study of the populations of our food fishes. The parts played by the nature of the organic and inorganic environment, and in particular the role of competition, presents problems for solution by careful observation and experiment.

Table I. Analysis of conditions for *L. ramada* fishery in Lake Mariut.

	1920	1928	1929	1930	1931	1933
Fry introduced (millions)	4·698	20·884	17·734	51·100	10·225	4·101
Total Catch (metric tons)	47·604	133·006	64·751	26·666	33·700	36·934
Aug.–Dec. catch (metric tons)	47·604	31·355	31·587	17·580	11·110	13·525
O group % by weight in Aug.–Dec. catch	100·0	42·0	23·4	23·4	23·8	17·2
Estimated numbers of O group caught (millions)	0·952	0·411	0·147	0·065	0·038	0·031
Fry for each O group fish caught	4·73	50·8	120·6	786·0	269·0	132·1
Mean length of O group fish	18·0*	16·3	18·8	21·2	20·9	21·3

* Mid-point of size range mentioned by Paget in the text of the Egyptian Fisheries Report for 1921.

Table II. Age, length and weight distribution of *L. ramada* samples from Lake Mariut.

	Age groups	*O*	*I*	*II*	*III+*	*Total*
1928 Aug.–Dec.	Numbers	184	85	15	9	293
	Mean length (cm)	16·3	20·9	21·5	20·3	
	Mean weight (g)	32	75	77	67	
	% weight of sample	42·0	45·5	8·2	4·3	
1929 November	Numbers	162	200	98	20	480
	Mean length (cm)	18·8	21·7	22·5	22	
	Mean weight (g)	50	80	90	84	
	% weight of sample	23·4	46·2	25·5	4·9	
1930 November	Numbers	41	53	36	6	136
	Mean length (cm)	21·2	22·0	22·9	22·7	
	Mean weight (g)	63	84	96	94	
	% weight of sample	23·4	40·3	31·3	5·0	
1931 November	Numbers	44	62	24	5	135
	Mean length (cm)	20·9	23·4	25·1	25·7	
	Mean weight (g)	70	101	123	132	
	% weight of sample	23·8	48·2	22·0	5·0	
1933 November	Numbers	21	63	18	1	103
	Mean length (cm)	21·3	22·3	24·0	26·5	
	Mean weight (g)	76	88	110	146	
	% weight of sample	17·2	59·8	21·4	1·6	

REFERENCES

Bromhall, J. D. (1954), A note on the reproduction of the Grey Mullet, *Mugil cephalus* Linneus. *Hong Kong Univ. Fish. J.*, **1**, 19–34.

Mortimer, C. H. (1954), Fertilizer in fishponds. *Colonial Off., Fish. Publ.*, **5**, 1 155.

Various Authors. (1922–1926), *Reports on the Fisheries of Egypt*, 1920–1935. Government Press, Cairo, Egypt, Page references not given here because 16 volumes are involved.

Wimpenny, R. S. (1936), The ova and larvae of *Mugil capito* Cuv. from Lake Qarun, Egypt. *Ann. Mag. Nat. Hist.*, (10), **17**, 405–412.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 257-260.

The mortality rates of Antarctic fin whale stocks

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IN 1820, WILLIAM SCORESBY, Jr., advanced the theory that the transverse striations occurring at regular intervals on the surface of the baleen plates of a whalebone whale afford an intimation of the age of the whale. ESCHRICHT and REINHARDT (1866) did not agree with this proposal, although they did agree that the striations were due to a periodicity in the growth of the plate.

Stimulated by the need for a method of making individual and direct age determinations of whales, we have studied the surface structure of the baleen plates and their possible application to age analyses since 1939. At the same time and quite independently, A. G. TOMILIN (1945) examined baleen plates in the collections of Russian museums.

In a series of papers (RUUD, 1940, 1945; RUUD and JONSGÅRD, 1950), we have shown that the transverse striations of the baleen plates are due to variations in the thickness of the cortical layer or enamel. We have also described how records made of these variations reveal growth periods which we have assumed to be annual. On this assumption we have developed a method for age analyses. The method has limited applicability because the baleen plates are subject to wear at their distal ends and therefore growth periods are gradually worn away.

We believe, however, that the age of fin whales in their first, second, third and fourth years (age groups O, I, II and III) can be determined with great exactitude, because of the presence of structures on the distal portion of their baleen plates, which indicate that this part was formed during the suckling period or during the first krill-feeding season. We assume further that our analyses of records from baleen plates of whales in age groups IV and V give fairly accurate results. Admittedly we can give only minimum estimates of the ages of older animals, because at some undetermined age the annual growth increment of the baleen plates is balanced by the annual wear at the tip; from then on we find a maximum number of 4 to 7 growth periods in the plates. Hence, our age groups above V should more correctly be VI +, VII +, and VIII +, meaning that older animals are telescoped into our three highest baleen-record groups.

For some years we have engaged in age studies of Antarctic fin whales. The material consists of baleen samples from catches of Norwegian pelagic expeditions in post-war seasons. Details concerning the material, analyses and results will be published shortly in *Hvalradets Skrifter* by HYLEN, PIKE, JONSGÅRD and RUUD. The histogram (Fig. 1) shows the percentage age distribution of the Antarctic fin whales taken during this period. In 1945/46 and 1946/47 our samples were small. It is therefore questionable whether they were representative of the catches, but since 1947/48 we have determined the ages of 850 to 1250 fin whales each season. Chi-square tests on length distributions show that our samples from the last six seasons are fairly representative of the catches from which they are drawn.

In the history of whaling there is ample evidence that whale stocks are easily overfished and depleted, if not to extinction, at least to such a degree that whaling is rendered unprofitable. It is only natural, therefore, that we, who have witnessed the gigantic expansion of modern pelagic whaling operations in the Antarctic, are on the alert for signs of over-fishing of the stocks of blue and fin whales. Such signs are now evident: (1) increasing numbers of small and sexually immature whales in the catches which result in a decrease in the mean length, indicate a corresponding decrease in the average age and (2) decreasing catches per unit of effort threaten the economy of the industry. This trend is influenced to some extent by the changes in the varying regulations imposed on the industry. Hence, although the trend seems to be unmistakable, the extent of the depletion may well be disputed.

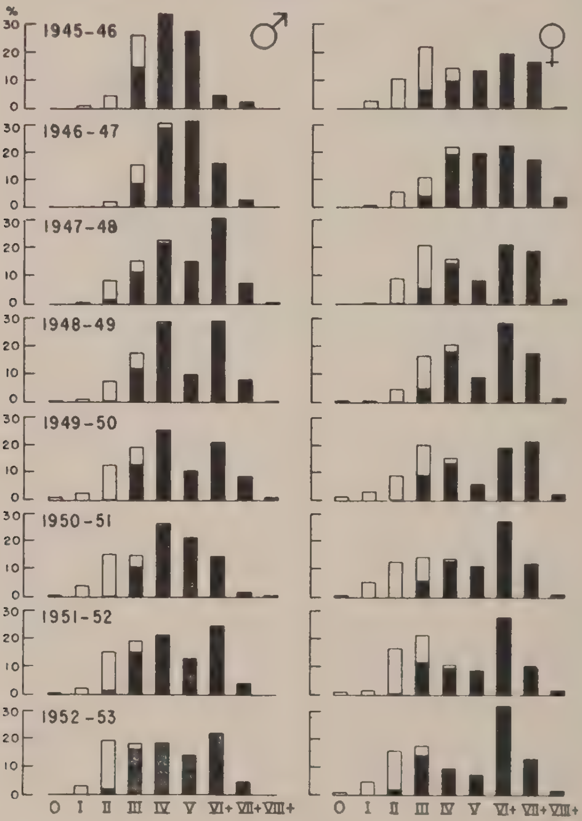

Fig. 1

It is agreed that carefully planned and extensive marking experiments may produce conclusive evidence of over-fishing, because the rates of fishing can be estimated from the rates of recovered marks. However, extensive whale marking is costly and there are great losses in the recoveries. Many marks are probably shed before recapture, and marks are easily overlooked when the whales are worked up. It would be better therefore, if the age composition of the catches were known, because, as shown by BARANOV (1918) and others, the right limb of the curves representing the age frequencies of the catches enables us to calculate the total mortality rates, provided that the following conditions are satisfied:

1. For the age groups in question, the mortality rate, or its complement, the survival rate, is uniform.
2. In these age groups, the samples used for age analyses are representative of the stocks.
3. The recruitment is uniform over a period of years; that is, each age group in question was initially of the same numerical strength as each of the others under study.

The first condition is satisfied as a rule in all stocks subject to high rates of fishing. As mentioned above, the second condition is satisfied fairly well for the last six seasons in our series. For the third condition, we can safely rule out the possibility that the recruitment to the stocks is increasing from year to year. The best we can hope for is a constant recruitment, or a recruitment fluctuating from year to year around a constant average sufficiently high to balance the losses from natural causes and from whaling operations. On the other hand, if the recruitment is decreasing, as it well may be, then the mortality rates calculated from the age distributions will be too low.

From the age distributions in Fig. 1, it can be seen that only groups IV and V of males and possibly groups III, IV and V of the females can be used in a direct calculation of survival or mortality rates. Thus, the ratios of Vs to IVs calculated for the period 1947/48 through 1952/53 give annual mortality rates which vary considerably from season to season, from a minimum of 0·17 (females, 1951/52) to a maximum of 0·65 (males, 1948/49). The means for the period are 0·42 and 0·40 for males and females respectively. Great seasonal variations might be expected if there were great fluctuations in the numerical strength of the year classes. This seems unlikely in a mammal such as a whale.

Systematic errors in our interpretation of the baleen records may, however, result in over-emphasis of age group V, because some older animals may be placed in that group. Such mistakes might vary in number from season to season. If this is the case, the calculated mortality rates will be lower than the actual ones.

Consequently, it is desirable to develop a formula which enables us to consider the total material contained in the right limb of the age-distribution curve. This is possible if we assume that the older animals telescoped into our age groups VI+, VII+, and VIII+ should in reality be spread in a regular way over a number of older age groups.

Thus such a formula for the annual mortality rate is: $a = 1 - \sqrt{\frac{A + B}{B}}$, where A is the sum of two age groups supposed to be fully represented in the catches, and B the sum of all higher age groups: hence, $A + B$ is the sum of all age groups considered.

We have formed the sum A from age groups III and IV of the females, and IV and V of the males, and used it in calculating the mortality rate for the individual seasons. These results show much less seasonal variation; namely a minimum of 0·19 and a maximum of 0·34 for females, and a minimum of 0·29 and a maximum of 0·49 for males. The mean mortality rate for the period 1947/48 through 1952/53 is 0·22 for females and 0·34 for males, with 0·28 *as an average for both sexes*. It should be borne in mind that this is either the true mortality rate, or, what is more likely, it is too low.

It is assumed that the female fin whale has her first pregnancy at an age of 3 or 4 years, and that she gives birth to one calf every second year. The maximum rate of increase for the stocks of fin whales should thus be 0·25 per adult per year. We know nothing about the annual mortality rates of immature age groups, but most likely they are considerable, because some will be taken in whaling operations (compare the left limb of the age distribution curves). It must be assumed, therefore, that the real rate of increase for the whole stock of fin whales must be significantly lower than 0·25 per year.

Since the annual mortality rate calculated above was 0·28 or more, the inevitable conclusion is that the Antarctic stocks of fin whales were overfished in the period 1946/47 through 1952/53. In that period the annual catches were about 21 thousand fin whales. In subsequent seasons they have increased to more than 27 thousand fin whales per year. Unless the stocks have increased, this means increased mortality rates also, and the stocks are being heavily overfished.

REFERENCES

BARANOV, F. I. (1918), On the question of the biological foundation of fisheries. *Bull. Bur. Fish., Petrograd*, **1** (1), 81–128.

ESCHRICHT, D. F., and REINHARDT, J. (1866), On the Greenland right whale. In: *Recent memoirs of the Cetacea*, London, 1–143.

RUUD, JOHAN T. (1940), The surface structure of the baleen plates as a possible clue to age in whales. *Hvalradets Skrift*. **23**, 1–24.

RUUD, JOHAN T. (1945), Further studies on the structure of the baleen plates and their application to age determination. *Hvalradets Skrift*. **29**, 1–69.

RUUD, JOHAN T., and JONSGÅRD, ÅGE (1950), Age studies on blue whales taken in Antarctic seasons 1945–46, 1946–47 and 1947–48. *Hvalradets Skrift*. **33**, 1–66.

SCORESBY, W., Jr. (1820), *An account of the Arctic regions*. Edinburgh, **1**.

TOMILIN, A. G. (1945), The age of whales as determined from their baleen apparatus. *C.R. Acad. Sci., U.S.S.R.*, **49** (6), 460–463.

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Fish origins—fresh or salt water?

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Summary—There are discussed various general considerations entering into palaeontological study of the problem as to whether the early evolution of fishes took place in fresh or salt water. Opposite conclusions as to the typical habitat of Silurian fishes have been reached by the author and GROVE on American evidence, on the one hand, and GROSS, mainly concerned with European material, on the other. An attempt is made to reconcile this difference. Part may be due to the very different histories of the two continents in Silurian times. Close examination of the stratigraphy of European fossil fish localities suggests that many deposits which are often regarded as marine are of continental or near-continental nature. It is concluded that the evidence, taken as a whole, points strongly towards fresh waters as the common Silurian fish habitat.

INTRODUCTION

IT IS generally agreed that the early chordates originated, as in the case of all major animal groups, in the sea. But many of the more ancient geological records of fishes are from sediments of continental type, and the possibility that fish evolved in inland waters was long ago seen as a distinct possibility. T. C. CHAMBERLIN in 1900 noted theoretical considerations favouring a fresh water origin, but failed to give any detailed consideration of the actual fossil evidence. In 1923 MACFARLANE (a botanist!) wrote an entire volume attempting to prove the fresh water origin of fishes; but this cannot be taken too seriously as proof of the case, for the argument is a forced one in many regards, and MACFARLANE's general attitude is that of the King of Hearts in *Alice in Wonderland*—" Verdict first, evidence afterwards ".

Two decades ago I determined to make a study of at least a considerable body of the available fossil evidence. In this I associated myself with Dr. BRANDON H. GROVE. My own inclinations at the time were mildly in favour of the hypothesis of a fresh water origin; Dr. GROVE (a student of invertebrate palaeontology) favoured, on the contrary, an early marine habitat. Under the circumstances any conclusion, one way or the other, which we could jointly reach, might be reasonably considered as attained in objective fashion. We decided to restrict our study to an attempt to determine the environmental conditions surrounding all fish finds recorded from North American pre-Carboniferous rocks. Our upper time boundary was set for the reason that by the end of the Devonian there definitely existed both fresh and salt water fish faunas and there was no need to go further. We limited ourselves to North America in a belief that the American record would give us a representative sample of the total world assemblage without our being forced to a consideration of European localities—localities with which we were personally unfamiliar and concerning many of which we would have had difficulty in obtaining exact data.

The results of our study (ROMER and GROVE, 1935) led both of us strongly to the belief that the early vertebrates were continental forms and that Devonian and later marine types had invaded the seas from fresh waters. As summarized in the left-hand column of Table 1, all American Silurian finds were indicative of a fresh water environment; during the Devonian, however, there was an increasing trend toward the sea, so that by the end of that period a truly marine as well as a continental fish fauna had been established.

At the time that we were considering the fossil evidence, the same general question was approached from an entirely different direction through the kidney studies of HOMER SMITH; these are to be found summarized in various papers and books by that author (1932, 1936, 1953, etc.); his conclusions are briefly discussed in my text, "The Vertebrate Body" (1955). His studies furnish extremely strong proof that the early history of vertebrates was passed in fresh waters. It is well known that typical vertebrates cannot exist unless their blood and body fluids contain a specific series of salts in a given concentration which is considerably lower than that of sea water. The most generalized type of vertebrate kidney is a structure that functions most especially as a " pump " to rid the body of excess water rather than merely furnishing (as in the case of many invertebrate nephridia) a means for disposal of metabolic wastes.* Such kidneys are found in all fresh water fishes and amphibians. These animals live in an environment where death would ensue, owing to osmotic dilution of the salt content of their blood and body fluids, were not such a " pump " present to rid the body of excess water, thus keeping up a proper salt concentration. Salt water fishes live, on the other hand, in a water medium containing a higher concentration of salt than their body fluids and hence equally dangerous to existence. A marine fish must avoid the danger of becoming too salty in its body fluid content; it may do this either by conserving water or by excreting excess salt, or both. Actually two very different methods are found in the two major groups of marine fishes. Salt water bony fish have solved the problem by (1) the development of salt excretion in the gills, and (2) in many instances by kidney modification which reduces the water outflow. Sharks, in contrast, have retained the " pump " type of kidney present in fresh water forms, but nevertheless prevent excess salinity of the blood by a most unusual specialization—the retention of considerable amounts of urea in the blood, so that blood and sea water are in osmotic balance and hence loss of water through surface membranes (and consequent dehydration) does not occur.

These two contrasting types of marine adaptations are not derivable one from the other; the two can have as a common origin only the kidney type found in fresh water forms. This is, therefore, the ancestral type. Hence the ancestral fishes must have lived in inland waters, and sharks and bony fishes must have independently invaded the sea.

I had hoped, since the time of our earlier publication, to be able on some occasion to extend our palaeontological study to the European deposits, much richer in Silurian and Devonian fish localities than North America, but had hesitated to do so because of the amount of time it would have taken to familiarize myself with the complex stratigraphic situation involved. To my delight, this topic is now covered in an excellent comprehensive work by GROSS (1950). In this he summarizes the pre-Carboniferous fish faunas of the entire world; since but few finds have been made in continents other than Europe and North America, the major new contribution is his careful review of the numerous and varied European assemblages. As one topic, GROSS considers the fresh *vs.* the salt problem. Although he had previously voiced his belief in a marine origin for fishes (GROSS, 1933, 134, etc.), he nevertheless treats the matter in a properly objective fashion. All finds from each locality are listed by genus or species, his conclusion as to the marine or continental nature of the desposit is stated, and totals for the two environments are computed.

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* *Amphioxus* is remarkably similar to the vertebrates in almost every basic feature, and practically every student of vertebrate history agrees that this little marine chordate is closely related, in some fashion or other, to the primitive vertebrates. *Amphioxus*, however, does not have a kidney of vertebrate type, but in contrast has nephridia comparable to those of certain marine organisms quite unrelated to the vertebrates. For this reason SMITH (1953) has felt forced to deny the relationship of *Amphioxus* to the vertebrates—this despite the strong evidence to the contrary seen in almost every other structural regard. This attitude seems to me quite unnecessary; in fact this contrast in kidney structure can be fitted satisfactorily into the assumed history. Although I am not aware of any precise functional study of the *Amphioxus* nephridia, these little organs appear to be (like comparable structures in many other invertebrates) primarily for the elimination of nitrogenous wastes, and not too efficient as eliminators of water. With the invasion of fresh water by the ancestral vertebrates, water elimination in quantity was a basic necessity, and the vertebrate kidney was evolved *de novo* as a water pump. But the kidney can also act as an eliminator of waste, and if nephridia were present in the fish ancestors, they could be done away with in safety once the new kidney mechanism was established. Thus the presence of nephridia in *Amphioxus* need not debar this animal from the vertebrate " family circle ".

For comparison, I have listed his summarized figures for the Silurian and the three subdivisions of the Devonian parallel to my own in Table I. For the Devonian stages we are in complete agreement. We both find that in the early Devonian, fishes were dominantly continental in habitat, but that there was a strong trend toward establishment of an important marine fauna before the end of the period.

As regards the Silurian, however, there is radical disagreement between our two studies. The American " sample " suggested that Silurian fishes were nearly or completely fresh water in habit, with the first marine invasion taking place only about the beginning of the Devonian. GROSS, on the other hand, believes Silurian fishes to have been predominantly marine; following this, his figures indicate that there was a sharp shift to a fresh water life in the early Devonian and then a strong reverse trend toward the sea.*

It is to a more detailed consideration of the European Silurian record that (following consideration of some general questions) the present paper is devoted. Not so much

Table I

Percentage of forms in seemingly fresh water deposits at successive horizons. Left, ROMER *and* GROVE (1935) *for finds from all North American localities*, right, *for world totals by species as given by* GROSS (1950, *table IV*)

	ROMER *and* GROVE	GROSS
U. Devonian	29	50
M. Devonian	13	64
L. Devonian	77	81
U. Silurian	100	36

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* The sharp marine-continental shift indicated by GROSS's figures would be further accentuated if the American finds were excluded and if, as is done by many workers today, the Downtonian and its equivalents were included in the Devonian. In this case, the apparent increase in fresh water fishes from Upper Silurian to Lower Devonian instead of being from 36 per cent to 81 per cent would have been from close to 0 per cent to about 90 per cent!

because of my own limited work on the fossil evidence as because of the seemingly conclusive nature of the evidence from kidney studies, I find it difficult to accept the conclusion to be drawn from GROSS's figures that fishes were entering fresh waters in major numbers for the first time at such a late period in the evolution as the end of the Silurian. Further, I find it difficult on ecological grounds to conceive of circumstances under which a sudden and almost unanimous surge of fishes from the ocean into the streams at the end of the Silurian would be immediately followed by a Devonian reverse migration of nearly as strong an intensity. An inquiry into the nature of the supporting evidence seems warranted. The reader, however, must be warned that this present inquiry lays no claim to the objectivity in treatment which I believe was true of the work in the ROMER–GROVE paper. Our conclusions there favoured a fresh water origin, but were, of course, far from definitive; the evidence for this same conclusion based on kidney structure is, however, of so substantial a nature that I am firmly convinced of its validity and hence find it difficult to believe that the palaeontological evidence truly indicates the opposite conclusion. The present discussion is thus, frankly, an attempt to reconcile GROSS's presentation of the Silurian fauna with the—to me—more probable thesis that the ancestral vertebrates (and hence presumably those of this period) were in the main fresh water forms.*

GENERAL CONSIDERATIONS

There may be noted here certain of the problems and difficulties encountered in attempting to evaluate the environment of early fishes. Most of the factors concerned (to my anguished regret) increase the difficulty of gathering evidence in favour of a fresh water origin.

Paucity of early continental sediments

If we were concerned with Tertiary deposits, a solution might be much more readily attained. From the late Cretaceous onward the fossil record includes not only abundant marine beds but also numerous formations of a definitely continental nature. But, as even an elementary consideration of geologic history would suggest, the continental record becomes increasingly scanty as we travel backwards in time. Period by period, successive cycles of erosion have tended to do away with inland and upland deposits, so that for the older epochs the sediments preserved include very few truly continental beds. The Mesozoic record of fresh water and terrestrial life is a fragmentary one. In the Upper Palaeozoic, extensive continental beds are rare, although they may be preserved in a few relatively stable areas, such as the South African Karroo. Going back to the Lower Palaeozoic, the elapsed time for the operation of diastrophic and erosional forces has been so great that practically no truly continental beds of that age survive today; the record is almost entirely marine. Our knowledge of the possible continental life of the Silurian and older periods is thus essentially confined to the inferences which may be drawn from such few marginal deposits, of deltaic and other coastal regions, which have alone survived.

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* It would be unfair to be unduly sceptical of the reality of the " double shift ", salt-to-fresh-to-salt, which GROSS's statistics would indicate, unless the data be broken down into its components. Might it be that this seeming anomaly has no real existence, and that the shift in the statistical totals is caused by changes in abundance of various groups and by the appearance of new groups which alter the total complex of the fauna without themselves changing notably in their environment? If the faunal components in GROSS's Table IV be considered separately, it will be seen that of the major groups present in the Silurian, the ostracoderms (Agnatha), show no reversal of trend. However, the two remaining Silurian groups, the acanthodians and arthrodires which together form a large percentage of the statistical material, show, in GROSS's table, a very sharp reversal.

But while the rarity of ancient deposits of typically continental type makes it difficult to establish the presence of fishes in early fresh water, this very condition in itself affords strong support to the fresh water hypothesis. A startling feature of early fish history is the way in which, in late Silurian and Devonian times, one major group after another appears on the scene quite suddenly and yet fully differentiated, with little or no trace of ancestors in earlier deposits. The most reasonable explanation of this remarkable situation is that the early evolution took place in inland waters, and that our dearth of knowledge is due to the dearth of ancient continental sediments.

Importance of negative evidence

Seeing our newspapers filled with reports of murders, robberies, suicides and the like, we sometimes lament the fact that the reader of such journals tends to gain the impression that all men lead lives of violence, whereas in reality nearly all are peaceable citizens leading humdrum lives that are not at all newsworthy. The case of the pre-Devonian vertebrates is quite comparable. Proponents of a marine origin point with pride to the occurrences of vertebrates in relatively small numbers in a limited series of Silurian marine—or supposedly marine—deposits. What is not remarked is the much more important fact that in the vast majority of Lower Palaeozoic marine formations there is not the slightest trace of any vertebrate. Such marine deposits are widespread and highly developed, and frequently carry abundant invertebrate faunas—but no vertebrates.

If the early vertebrates were marine, why are they not commonly found in such beds? A variety of possible explanations has been advanced by proponents of marine origins and may be briefly discussed, seriatim. (1) *Since vertebrates are relatively rare in marine beds, lack of specimens is due to the chances of random collecting.* But this is unsatisfactory; in all post-Silurian periods, vertebrates, although seldom common, are nevertheless found in a great variety of marine beds. (2) *Vertebrates did not evolve until the time when we begin to find them in marine beds.* But vertebrates are known well down in the Ordovician. (3) *Vertebrates were present earlier, but did not develop a hard skeleton until late Silurian times.* But the few known Ordovician vertebrates were already well ossified. (4) *Vertebrates were present in the ancient oceans, but acquired a bony skeleton capable of preservation only when they invaded fresh waters.* This is a rather better argument. One thesis is that there might have arisen on entrance to fresh waters some physiologic condition causing deposition of calcium salts in the dermis. But the armour of ancient ostracoderms and placoderms is of varied and complex patterns, not a mere random deposition of calcium, and later fishes show no sign of physiologic discrimination between fresh and salt water as regards degree of ossification. I have myself aided the argument somewhat by the suggestion (ROMER, 1933) that vertebrate armour was important in defence against eurypterid enemies. Perhaps armour did arise on entrance into fresh water in connection with defence. But unless we believe that bone arose independently a very considerable number of times in the vertebrates, this does not aid the marine argument. And finally, under this sub-topic: if it be argued that presence of bone and fresh water life are correlated in early vertebrate history, claims that most Silurian vertebrates with armour were marine must be abandoned—" one cannot eat one's cake and have it too ".

Although believing strongly in a fresh water origin for vertebrates, I must confess I am surprised, not at the fact that there are a certain number of reports of reputed marine vertebrates from the Silurian, but rather at the fact that, when such reports are carefully scrutinized, there are so few instances of unquestionable marine occurrences. During the Devonian and later periods there were various incursions from fresh water into the sea; similar incursions of ostracoderms may well have occurred earlier. The record suggests that, on the whole, the Heterostraci were a relatively euryhaline group and may have had marine representatives in the Silurian, as appears rather definitely to be true in the Devonian.

Biocenosis vs. *necrocenosis*

Our object is to determine the conditions under which the early fishes lived. Study of the beds in which fossil remains are found does not necessarily tell us this. Habitat in life and place of burial may be far removed from one another. If a cadaver is destroyed by predators, its remains may be buried on the spot. But if the trunk of a dead fish remains intact, gradual decomposition results in buoyancy, and the cadaver may be transported by currents far from its proper habitat before settling to the bottom. The fact that water runs down hill works strongly to the detriment of one advocating a fresh water origin. An inland stream-dweller will tend to be carried down to lower reaches of a river system; forms living in a coastal region may be carried out to sea, with resulting ecological confusion. If fish specimens in a given formation are abundant and well-preserved, a life habitat in or close to the spot where they are found is strongly indicated. If rare and fragmentary, remains in a marine deposit strongly suggest transportation by currents; but whether transportation from another marine locality or from fresh water cannot, of course, be proven.

Identification of fresh water deposits

Marine sediments are frequently identifiable in ready and positive fashion; there is generally an abundance of invertebrates of dominantly marine groups. Identification of Palaeozoic fish-bearing beds as continental in nature is a much more difficult task, for the evidence is essentially negative in nature. Sediments are no sure guide. While limestones are highly suggestive of marine conditions, calcareous deposition may take place in inland waters, but on the other hand shales and sandstones, although presumably derived ultimately from continental areas, have been in large measure deposited under marine conditions. It is only in the case of coarse clastics and conglomerates that continental conditions, or an approach to them, are strongly suggested by sediments. As to the associated fauna, the absence of typical marine invertebrates suggests continental conditions. This does not, however, prove the case, for there are numerous marine areas today in which invertebrates capable of fossil preservation are absent, and there are numerous geologic formations which were obviously laid down in a marine situation and yet contain few or no invertebrate remains. Further, absence of marine fossils in fish beds may be attributed by those advocating salt water environment to diagenetic removal, by solution, of carbonate shells once present. But this argument is one of which one may be reasonably sceptical if used too frequently.

In many Devonian beds which are generally agreed to be of a continental nature we find fishes associated with a sparse fauna including eurypterids, ceratiocarid crustaceans and very little, if anything, else (plant remains of probable fluviatile or terrestrial nature may be present as well). There are various Silurian deposits with a similar assemblage, and in default of evidence to the contrary, it is reasonable to consider them likewise continental in nature.

Need for detailed stratigraphic study

If a geologic formation or group is dominantly marine (or continental) in nature, it is frequently claimed that the fossil forms contained in it at every horizon must be entirely marine (or continental) in origin. Such statements should not be made or accepted without careful consideration of stratigraphic detail and possible facies differences. For example, the early Permian Redbeds of north central Texas in which I have worked extensively, are predominantly continental, with a wealth of terrestrial reptiles and fresh water amphibians and fishes. But it would be absurd for me to make a sweeping claim that all the fossil content of these beds (which includes, for example, a number of cephalopods) is of a continental nature. The deposit is a deltaic one, and from time to time the delta was invaded for a brief period by waters from a sea which lay not far away. When in doubt, it is thus important to know, in the case of such a continental formation, the exact horizon and locality from which a fossil has come before attempting to reach conclusions as to its ecologic position.

The same caution should be observed in the case of fossils contained in a dominantly marine formation or zone—particularly so for fossils of the time under special consideration, the late Silurian, when over much of Europe there was occurring a transition from marine conditions to the continental " Old Red " of Devonian times. We are dealing with " Passage Beds ", tending toward and reaching deltaic conditions, where fluctuations of a very minor nature could readily cause alternations of salt and fresh water environments. Close examination of stratigraphic detail is requisite if the truth is to be sought for.

Fresh and brackish water invertebrates

Most invertebrate palaeontologists working in the Palaeozoic are dealing with marine faunas, and hence generally tend to assume, unthinkingly, that all Palaeozoic invertebrates are unquestionably marine. This was obviously not the case; there is an acknowledged, if small, fresh water fauna of invertebrates in the Carboniferous, and there is every reason to believe, on theoretical grounds, that at whatever earlier date a basal plant food supply had been established, an invertebrate fauna would have soon evolved to occupy this ecological niche. Before the close of the Devonian a continental flora of rather advanced and diversified nature was present. This must have had an antecedent history of some length. It is not necessary, however, to wait for the development of land floras to establish a fresh water biocenosis, and it may well be that fresh waters may have contained, as far back as the Cambrian, at least, a basal element in a potential food chain in the form of simple algae.

Two problems, among many, which must be " solved " by any type of animal which attempts to leave the ocean and avail itself of the opportunities offered by a life in fresh waters, are: (1) physiological adaptations to counteract dilution of body liquids (with resulting death) in non-saline waters, and (2) some method—preferably active locomotion—for maintaining the population in an inland environment and preventing adults or young from being carried downstream, back the ocean.

The modern fresh water invertebrate fauna is relatively sparse as compared with that of the ocean, but contains a considerable variety of types. As would be expected, sessile forms, and those with relatively poor locomotor ability, such as sponges, coelenterates, bryozoans and brachiopods are rare or absent; the molluscs, however, have achieved success by means of highly specialized modifications of developmental processes. More common are active-swimming bilaterally symmetrical forms including (in addition to fishes) a variety of members of the worm phyla and, most especially, diversified crustaceans, mainly phyllopods, cladocerans, copepods and ostracods. In addition to truly fresh-water assemblages, there are, of course, a variety of other invertebrates derived from both marine and inland faunas which are euryhaline, able to live in brackish water deposits of the sort which may be encountered in estuarine and deltaic regions (cf. O'CONNELL, 1916, 70–76).

Although it seems certain that a fresh-water invertebrate fauna containing elements analogous to those present today was developed at an early stage, little attention has been paid to this subject by invertebrate palaeontologists. As in recent times, however, most of the forms present would probably have been soft-bodied, and hence not likely to be fossilized, or of small size and hence liable to escape observation. In the Devonian and Silurian fish-bearing beds which are reasonably suspected of being of fresh-water origin recorded invertebrates are few in number. There are occasional reports of lingulids, *Leperditia* and a few other forms which may indicate a brackish layer or a brief incursion of salt waters. Two invertebrate types, however, occur time after time with fishes—ceratiocarids and eurypterids. It may be reasonably claimed that they are fresh water in habitat or are euryhaline forms which were able to inhabit, with fishes, fresh water streams into which typical marine life could not extend.

The ceratiocarids are small crustaceans, apparently of phyllopod affinities, which have attracted little scientific attention. Study of them from an ecological point of view should prove interesting. *Dictyocaris* is another phyllopod which has a distribution likewise suggestive of fresh waters (STØRMER, 1934).

The eurypterids are the one group of Palaeozoic invertebrates which exhibit such distinctive features in their apparent ecological surroundings that students of invertebrate palaeontology have had to hesitate, at least, in their habitual tendency to claim a marine environment for all fossils. The eurypterid environmental picture is comparable in many ways to that for the older fishes, but with somewhat less evidence for fresh water habitats. We can here but briefly note the main points in the discussion; among the major papers concerned are those of O'CONNELL (1916), POMPECKJ, VERSLUYS and other discussants in a 1923 symposium, and RUEDEMANN (1934, etc.); a recent resumé is that of PRANTL and PŘIBYL (1948, 108–111). Eurypterids are most abundant in the Silurian: they are rare earlier, and although surviving until the Permian become increasingly uncommon from the Middle Devonian onward. The post-Silurian forms are definitely fresh water, and these, together with certain of the Silurian finds, are often associated with fish faunas which likewise appear to be fresh water in nature. In the Silurian, however, the eurypterids occur in a number of situations in which the evidence for a fresh-water habitat is far from certain (as the " water limes ") and, further, are present to some degree in beds of definitely marine nature. As PRANTL and PŘIBYL note, the " almost universally accepted opinion " today is that the eurypterids were fresh water organisms throughout their history. It appears to be rather generally accepted that occurrences of eurypterid remains in deep water deposits, such as graptolitic shales, are due to necrocenosis, the floating outward of cadavers or shed armour. But to Ruedemann and a minority of other workers, the number of occurrences of eurypterids in lagoonal and near-shore deposits suggests that the older Palaeozoic eurypterids were euryhaline, capable of living in sublittoral and neritic marine environments.

" *No decision?* "

The work on kidney structure and function makes it reasonably certain that fresh waters were the original fish environment. However, it is obvious from the discussion above, that it is difficult to reach a positive confirmation of this conclusion from palaeontological studies, no matter how carefully conducted. Additional points are sometimes advanced which tend towards the discouraging conclusion that attainment of palaeontological proof is not only difficult but perhaps impossible.

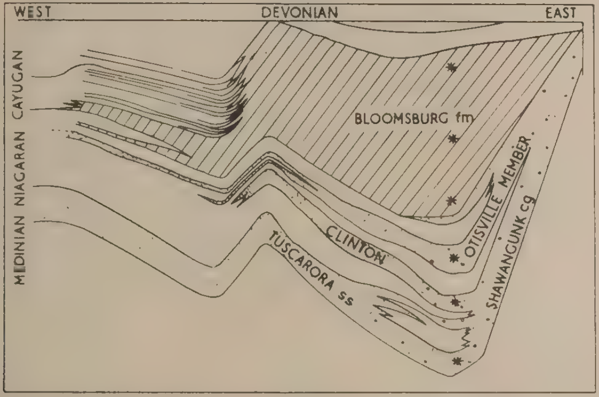

Fig. 1. Diagrammatic east–west section through the Silurian of Pennsylvania, showing the transition from sediments of continental type at the east to an essentially marine section at the west. Known Silurian vertebrate occurrences are all in the eastern continental region, and although not confined to a single area, are here shown in approximately their vertical and horizontal position. Conglomerates and sandstones stippled; redbeds (essentially continental) hatched; limestone and other typical marine beds unshaded. (Modified from Moore; data from C. K. and F. M. Swartz.)

It may well be, for example, that the available material of early fishes is too late in date to be of great value. We have little evidence to go on before very late Silurian days, while the Ordovician scrap material shows that ostracoderms were well developed by the middle of that period and probably originated at a much earlier time. There may, therefore, have been considerable ecological shifting between streams and sea by Silurian times, so that evidence from that period may have little meaning in terms of truly primitive vertebrate environments. Again, it is possible that Silurian fishes may have been to a considerable degree euryhaline in nature, with an ecologically cosmopolitan range; if such were the case, a distributional study would be meaningless. Still further, ontogenetic development must be considered. As Westoll (1945) has pointed out, it is probable that young ostracoderms had little or no armour, and hence cannot be found under normal conditions as fossils. In consequence we cannot tell where these " fry " lived; they may have stayed in the same environment throughout their lives, or may have migrated from salt to fresh waters or vice versa at the end of the larval period.

These are discouraging thoughts. But despite them, I feel it is nevertheless profitable to follow the known evidence as far as it can lead us.

THE EUROPEAN SILURIAN RECORD

We now come to the specific problem under discussion—the fact that, while the North American Silurian fish fauna, although limited in extent, includes a series of finds extending over the greater part of the duration of the Silurian which is almost purely fresh water in apparent origin, the European record of fishes is confined almost entirely to the closing phases of the period and, according to GROSS's interpretation, is dominantly marine in origin. How can these contrasts be reconciled?

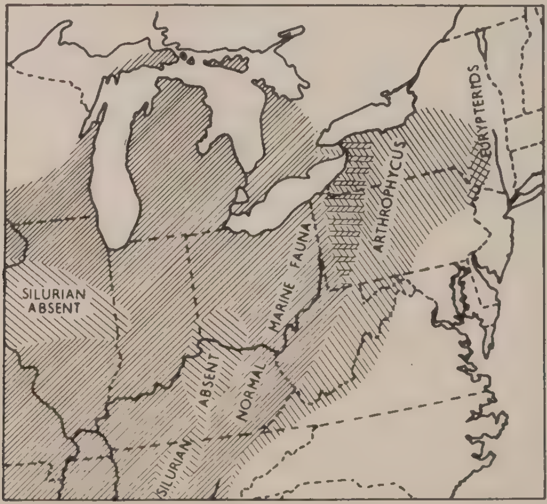

Fig. 2. A map of the north-eastern United States area in Lower Silurian times to show the distribution of some major faunal elements. The midwestern region was one of typical marine conditions, with limestone deposition dominant. Farther east, toward the presumed land area, is a transitional zone with few fossils except the problematical *Arthrophycus*. The most easterly zone in which Silurian sediments are preserved is a seemingly continental deposit of conglomerates and sandstones with a eurypterid-fish fauna. (From AMSDEN.)

Part of the differences may be readily accounted for if we review the differences in the Silurian history of the two areas. In North America, as may be seen from the summaries in any standard text (as, for example, MOORE, 1933, 159–177) the Mississippi Basin region was occupied throughout the Silurian by a sea. Along the eastern border of the present continent, however, there is believed to have been an area or areas of high land—the land mass of " Appalachia ", or an island chain. Throughout nearly the length of the Silurian period materials from this region were carried westward, to be deposited along the sea margins as conglomerates, sandstones and—particularly in late Silurian times—red shales. The gradual lateral change in sediments from eastern deposits dominantly continental in nature to western marine shales and limestones is well illustrated in the east-to-west section of deposits in Pennsylvania shown in Fig. 1, and the palaeogeography of the Silurian as a whole is well exemplified by the map for the early part of the period given by AMSDEN (1955) and reproduced in Fig. 2. The known vertebrates are present only in the most eastern and more definitely continental formations; there is no trace of any vertebrate in the marine beds to the west. This situation is in perfect agreement with the theory that the centre of distribution of the vertebrates of that day lay in fresh waters.

In Europe, the Silurian geologic story is in strong contrast with that of North America. For most of the period much of Europe was occupied by a widespread ocean, in which were perhaps a few small islands; the shores of this ocean lay far to the north and east (Fig. 3). Toward the end of the Silurian, however, the oncoming of the Caledonian Revolution brought about an advance of the shore-line to the south, over the areas indicated by cross-hatching on the map. This brought about the development in Downtonian times of beds of nearshore, estuarine and deltaic nature, leading to the characteristic Devonian continental deposits of " Old Red Sandstone " type. It is in this area of advance of the shore-lines and oncoming of continental conditions that nearly all of the European Silurian fish-bearing deposits, indicated by figures on the map, are to be found. The late appearance of fishes in the European Silurian is thus closely correlated with the late appearance of " transitional " or truly continental beds in which remains of fresh-water dwellers would be expected.

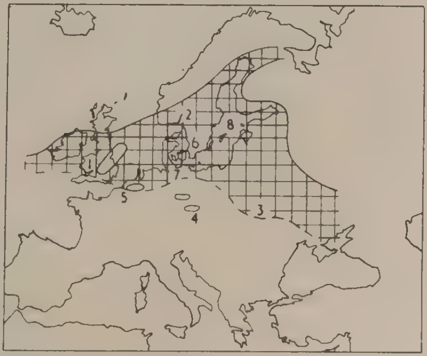

Fig. 3. Map of Europe to show changes in land–sea relations in late Silurian times. At the end of the Middle Silurian much of Europe was covered by a sea. Its northern shoreline (full line) is believed to have run along the northern part of the British Isles to central Scandinavia and then south-eastward through Finland and central Russia: islands are believed to have existed in England, in the region of the present Belgian coast, and in Saxony and Bohemia. By the end of the Downtonian, continental conditions had extended southward over much of northern Europe (cross-hatched area). The Silurian vertebrate localities (numbered) all lie within the area of advance of continental sediments or close to the island areas. (Modified from BORN.)

Of the deposits numbered on the map, numbers 1 and 2 are recognized by GROSS as continental. The remainder are considered by him as definitely marine. Let us briefly review the stratigraphic evidence concerning these deposits to test the validity of such a conclusion. In doing so, I will restrict discussion to the materials considered in GROSS's paper. As he has done, we will here include the Downtonian as part of the Silurian, although recognizing the growing tendency on the part of many stratigraphers to include it in the Devonian.

1. *Great Britain*

In Great Britain (JONES, 1929; KING, 1934, etc.) the Silurian was for most of its duration a time of marine deposition (Valentian, Wenlockian), and in correlation with this there are no vertebrates recorded until fairly late in the period. The upper Silurian Ludlow beds are likewise marine, but there are a few records of fragmentary vertebrate remains; English stratigraphers generally agree, however, that these are " strays " floated out from the shore-line of the advancing land areas at the summit of the Ludlow.

Vertebrates first appear in numbers in the famous Ludlow Bonebed, marking the arrival of continental conditions and the transition to the Downtonian. This last is obviously a deltaic formation. There are occasional eruptions of brackish to salt waters (as indicated by the presence of *Lingula*, etc.), but essentially it is a fresh-water deposit, with a paucity of invertebrates and a diversified fish fauna. As in many other Silurian and early Devonian continental deposits, the fishes are accompanied by eurypterids and ceratiocarids. The British record is thus consistent with beliefs as to the general fresh water nature of early fish faunas: fishes appear only as continental conditions are approached or reached.

2. *Norway*

Here again the fish record is clearly one indicating a fresh-water habitus. The Norwegian Silurian is restricted in area, and found mainly in the Oslo fiord region, as at Ringerike (KIAER, 1908, 1924; HEINTZ, 1939). In Norway, marine Silurian beds are, as in England, succeeded by continental " redbeds " comparable to the English Downtonian but possibly somewhat earlier in age. In these beds typical marine fossils are absent; as usual, the vertebrates are accompanied by eurypterids and ceratiocarids. There are no vertebrates in the marine part of the section; fishes appear when continental deposits appear.

3. *Podolia*

The late Gotlandian and " Passage Beds " of Podolia contain a considerable fauna of vertebrates—about 24 types, described by ZYCH (1927), BROTZEN (1933 A, 1936), and STENSIÖ (1944)—which are similar to those of the continental Downtonian. However, there is a considerable marine fauna in the Podolian beds as a whole, and hence these forms are classed by GROSS (46–49) as marine.

Let us, however, examine more closely the stratigraphic situation as described by KOZLOWSKI (1929, 1–23; more recently summarized by SAMSONOWICZ, 1950, 499–503). KOZLOWSKI distinguishes three successive Silurian stages. The lowest, the Skala stage, has a good marine invertebrate fauna; no vertebrates are present. In the second, Borszczów, stage there is likewise a good marine fauna. There are no reports of vertebrates except that BROTZEN (1936) mentions that indeterminate acanthodian scales have been found. The fish remains are thus almost entirely confined to a final stage, the Czortków, which is many ways comparable to the Downtonian, and is succeeded by typical continental Old Red deposits. KOZLOWSKI cites a considerable marine invertebrate fauna from the Czortków as a whole, but we should not jump to the conclusion that the fishes are intimately associated with this fauna. To cite (in translation) KOZLOWSKI's description (1929, 14) of the Czortków, in part: " In the lower beds . . . the fauna is composed mainly of brachiopods, tentaculites, little ostracods and pelecypods. In the upper beds . . . the tentaculites and the brachiopods diminish progressively in number, while the leperditiids and the fishes become more and more numerous. Finally, in the terminal beds . . . the brachiopods are very rare (with the exception of lingulas), the fauna being principally made up of ostracods, among which the leperditiids dominate, filling entire beds, and of fishes; here one also finds fragments of *Pterygotus*. This difference between the fauna of the lower part of the stage and that of its upper part has been remarked on by most of the authors occupying themselves with the Silurian of Podolia. . . . However, the passage from one fauna to the other occurs in a gradual manner, and certain species characteristic of the first continue in the second until its disappearance. . . . This underlines the unity of the Czortków fauna from its commencement until the moment when continental conditions have invaded the marine basin and put an end to its existence."

KOZLOWSKI further states, *in litteris:*

" Dans l'étage de Czortków, en allant de sa base vers le sommet, on constate un développement de plus en plus accentué du facies schisto-gréseux. Ce que BROTZEN appelle ' Uebergangsschichten ' et ' Schichten mit grünen Sandsteinen ' correspond à la partie supérieure de la série de Czortków qui est séparée de sa partie moyenne par un épais banc de grès micacé. A partir de ce banc les grès et schistes dominent de plus en plus sur les calcaires à faune marine, ces derniers ne formant que de minces intercalations dans la série schisto-gréseuse. Il me semble qu'on y a à faire à un empiétement de plus en plus accentué du milieu continental sur le milieu marin. Et il est significatif qu' à ceci correspond un enrichissement progressif des sédiments en restes de Vertébrés, surtout de Ptéraspidés. Aujourd'hui—toutes mes notes ayant disparu pendant le guerre—je ne saurais dire si ces Vertébrés se rencontrent seulement dans les couches de schistes et de grès ou s'ils se présentent également dans les intercalations calcaires à faune marine. Quoiqu'il en soit on a l'impression que leur présence dans le série de Czortków est essentiellement liée aux avancements périodiques des dépôts deltaïques dans le domaine marin. On y observe aussi que dans les intercalations marines, en allant du bas vers le haut de la série, les Brachiopodes sont progressivement remplacés par les Lamellibranches et surtout par les Ostracodes."

No extensive comment is, I think, needed. We have here an excellent example, in an area towards and over which continental Old Red deposition was advancing, of a transition from typical marine beds to brackish, presumably estuarine deposits, and to continental redbeds, much as in England or Norway. As in those countries, fishes appear in numbers only as continental conditions are approached. Far from indicating a marine fish habitat, the Podolian situation strongly supports the thesis that fresh waters were the centre of Silurian vertebrate life.

4. *Bohemia*

We are here beyond the limits of the Downtonian advance of continental deposits from the north, but it appears that although much of Bohemia was covered by seas during the Silurian, there was present here an island area (cf. Fig. 3) which was the nucleus from which a larger land mass emerged in Devonian times. The Bohemian

Silurian includes " Bandes " Ee$_1$, Ee$_2$, and Ff$_1$ of Barrande, termed eα, eβ and eγ by KETTNER and KODYM (1919) and BOUČEK (1934). A certain amount of fish material is present which, as GROSS notes (1950, 64–65), is as yet insufficiently described. GROSS states that the beds containing fishes are " all of purely marine origin " and hence counts all the Bohemian fish as part of his Silurian marine assemblage. A closer examination of the actual sequence, however, suggests a somewhat different interpretation. The stratigraphy has been most recently reviewed by PRANTL and PŘIBYL (1948, 67–73). Zones eα and eβ, which cover most of the extent of the Silurian, appear to be typically marine. There are no described fish except for one and possibly two spines of *Onchus*, with one of which some scales are associated; these are most reasonably regarded, like the equally rare fragments in the English Ludlow and in the Borszczów of Podolia, as strays from the adjacent land area.

In eγ, the " Lochkov Limestones " there is a diversified fish fauna, although specimens are not abundant. Much of the Lochkov exposures show a typically marine reef facies; the fish, however, occur instead in a shaly facies in which a series of successive zones are present (PERNER, 1918 A, 1918 B; PERNER and KODYM, 1919, 1922; PRANTL and PŘIBYL, 1948, 73). This facies is stated to be limited chiefly to a seam in the Radotin Valley between Prague and Kosor. The fish described by PERNER occur in the lowest zone. PERNER and KODYM (1922, 67) state that in this zone " other fossils are also rare "; since they give detailed faunal lists of invertebrates from all other Silurian horizons but name no invertebrates from this zone, it would seem that any non-vertebrate material present is inadequate to give evidence regarding ecological conditions. Following the fish zone is a layer of black bituminous limestones with thin intercalated shales, the lower part of which contains eurypterids and ceratiocarids but no other fossils. Above this, the remainder—and greater part—of the shaly facies contains typical marine invertebrate assemblages.

We have, thus, in the lower zones of the shaly facies of the Lochkov the familiar story of fishes, eurypterids and ceratiocarids with little or no indication of a marine invertebrate fauna. Far from indicating a typical marine environment for the Lochkov fishes, the evidence strongly suggests that their place of entombment was a near-shore and possibly deltaic deposit.*

5. *Pas-de-Calais*

A second " island " region, independent of the advance of the main Downtonian continental shore-line, is that of the Pas-de-Calais region of northern France. Here, LERICHE (1906) has described from the late Silurian or Downtonian of pit number 6 of the Liévin mining company of Pas-de-Calais two species of Heterostraci which GROSS appears to include in his marine list. The beds *as a whole* do contain good marine fossils: but LERICHE (18–21) gives the section in detail, as shown below. This definitely indicates that the fishes are not associated with the marine invertebrates. The figures given are depths from the surface, in metres:

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* Mr. RADVAN HORNÝ, of the Geological-Palaeontological Institute of the Charles University and Dr. FERDINAND PRANTL, Vice-Director of the Národní Museum (Prague), in letters received after completion of this paper, have furnished further information with regard to this situation. They feel certain that these beds are all marine in nature, but that, on the other hand, the fragmentary and isolated condition of the fish remains indicates a necrocenosis, with post-mortem transportation from another habitat—quite possibly, of course, fresh water. It is obvious that the Bohemian fish faunas are of great interest, and it is to be hoped that our Czech colleagues will make a thorough study of them

to 270·70 Typical Old Red sandstone (Gedinnian) with ostracoderms
270·70 to 295·80 Sandstones more drab than those above, micaceous, somewhat calcareous; *Cyathaspis barroisi* at 278–281; no other fossils reported
295·80 to 296·30 Dark blue schistoid sandstone with marine shells
296·30 to 298 Pale grey sandstone with *Pteraspis gosseleti*
298 to 318·20 Dark blue schistoid sandstone with marine shells
318·20 to 331·70 Pale grey sandstone with *Pteraspis gosseleti*; a bonebed at base
331·70 to 350 Dark blue schistoid sandstone with marine shells
350 to 473 Marine beds of Ludlow age, with *Dayia navicula*, etc.

The section here is clearly comparable in its general nature to a typical English section—first marine Ludlow beds; then " Passage beds " in which final marine phases alternate with non-marine ostracoderm layers, including an initial bonebed; these are followed in turn by a typical Old Red sandstone of continental type.

6. *Scania*

The remaining European vertebrate localities are from the Baltic region. There are here excellent Silurian sections in the main typically marine in nature. As was true both to the north and west in Great Britain and Norway, and to the south in Podolia, we are in a region in which there was a change from marine to continental deposits at about the end of Silurian times. But although it is probable that typical " Old Red " deposits were formed in this area, none is preserved, and in consequence we are left to interpret the story from decapitated Silurian stratigraphic columns from which the terminal Old Red has been secondarily removed. Although the island of Gotland is the classic locality for study of the Baltic Silurian we shall use that of adjacent Scania instead, since but a single vertebrate specimen (not mentioned by GROSS) has been found in Gotland, whereas LEHMAN (1937) has described numerous scales, spines and other fragments from Scania.

In Scania we find a Silurian sequence comparable in nature to those we have described in other regions. For most of its vertical extent the Silurian is purely marine in nature, including *Rastrites*, *Cyrtograptus* and *colonus* stages covering the Valentian and Salopian. The last is succeeded by the Öved-Ramsåsa stage, generally equated with the Downtonian. As BORN notes (1926, 160), this stage contains few invertebrates. " Es handelt sich hier um eine typische verarmte Fauna der Übergangsschichten, die zum kontinentaler Old Red überleitet." The Öved-Ramsåsa is composed mainly of coarse clastics. Limestone is found only in the lowest of four zones; it is followed by barren white and yellow sandstones; then by grey-blue clays containing fishes and eurypterids and also a variety of invertebrates; finally by red sandstones containing nothing but *Lingula* and ostracods. The Öved-Ramsåsa is, thus, ecologically a Downtonian type of deposit. It is certainly no more marine in nature than an estuarine–deltaic situation, and even so, the fragmentary nature of the fish remains strongly indicates an upstream origin, with the remains, as LEHMAN suggests, brought to the area of deposition by currents. As far as I am aware, there are no published data showing the exact stratigraphic relation of the fish scales to the marine fossils contained in the same zone.

7. *The Beyrichienkalk erratics*

Among the numerous glacial erratics of the north German plain, a large percentage are derived from an upper Silurian formation termed the Beyrichienkalk which presumably was once widely developed in the west Baltic region but is now known only from erratics and deep borings (KRAUSE, 1877; ROEMER, 1885, etc.). A percentage of the erratics have yielded scales and other fragmentary fish remains, best described by GROSS (1947). From the nature of the case, the general stratigraphic situation cannot be determined, but the age is certainly quite late Silurian, and a general equivalence to the transitional Öved-Ramsåsa beds is indicated. This is further suggested by such ecological data as can be derived from the erratics themselves. In some cases, as the conglomeratic boulder described by BROTZEN (1933 B), there may be no fossils other than the scales themselves; in other instances the scales are interbedded with invertebrate fossils. The remains are always fragmentary and the situation suggests, as in Scania, transport from a more continental type of habitat into an estuarine or near-shore deposit.

8. *Oesel*

Most famous, most interesting, and most controversial of all Silurian vertebrate deposits are those of the Baltic island of Oesel, Esthonia, famous since the days of EICHWALD, PANDER, SCHRENK and FR. SCHMIDT. The stratigraphy has been reviewed by HOPPE (1931). The lower to middle Silurian beds of Esthonia—the G, H and I stages—are purely marine in nature and, as would be expected, have yielded not the slightest trace of a vertebrate. The uppermost beds are those of the K stage of Oesel. The fauna is particularly interesting from an evolutionary point of view as the only notable vertebrate assemblage in the world which is clearly pre-Downtonian in age. Considered as a whole, K has an abundant invertebrate fauna, and hence GROSS classes the numerous Oesel vertebrates as marine. As is generally the case, however, closer examination casts strong doubt on the truly marine nature of the vertebrate occurrences.

K is divided into four zones. K_1, the Rootziküll–Karmel Zone, is a dolomitic formation which varies considerably in facies both vertically and horizontally. At several horizons in the western end of the island, notably at Rootziküll and Wita, there are layers which carry an abundance of the familiar assemblage of eurypterids, *Ceratiocaris*, and a variety of ostracoderms—mainly cephalaspids with *Tremataspis* as the most common form. In the K_1 zone as a whole only nine species of presumably marine invertebrates are recorded. HOPPE (43) notes that in the *Eurypterus* deposits proper the only definitely marine forms recorded are an *Orthoceras* and very rare specimens of *Favosites* and *Conchidium*; whether these are exactly in the fish-eurypterid layers or merely stratigraphically close to them is not stated by him. O'CONNELL (1916, 143–147), after reviewing the earlier literature on this point says: " In summary, it may be said that the detailed sections bring out the sporadic occurrence of the eurypterids in very thin beds, rarely intimately associated with the typical marine forms which occur in beds above and below the eurypterid marls."

Quite in contrast is K_2, the Padel Zone. Here there is an abundant marine invertebrate fauna, mainly of brachiopods and stromatoporites; forty-five species are listed. It is not surprising to find that eurypterids are unknown and that of fishes there are only isolated and apparently very rare scales of one species of *Coelolepis*.

K_3, the Kaugatoma Zone, is, again, typically marine, with a fauna of forty-one invertebrate species. Eurypterids are absent; fishes are found somewhat more commonly than in K_2, but only in the form of isolated scales of *Gomphodus* and a few spines of the *Onchus* type.

In the K_4 or Ohesaare Zone, exposed only in a very restricted area of the island, we leave the limestone–dolomite formations typical of the lower zones, and find ourselves in a deposit characterized for most of its extent by a rapid alternation between thin limestones, typically crystalline and red in colour, and equally thin clay conglomerates; in a profile little more than 3 metres in thickness HOPPE distinguishes no less than 70 such alternating layers. The situation, as HOPPE notes, indicates that we are very close to the shore-line. There is a fairly good marine fauna in K_4 as a whole, including 34 species of invertebrates. There are no eurypterids. There are, on the other hand, numerous remains of fishes. But nowhere are there articulated specimens, the whole material consisting of isolated scales, spines and fragments of various types, and HOPPE notes that the fish remains are not normally associated with the marine invertebrates, but occur only in bonebeds at three specific horizons.

In attempting to review this interesting Oesel series, the most striking general feature of the story is the fact that the fishes and marine invertebrates are (so to speak) " allergic " to one another. The beds here follow the " rule of thumb " which we have seen to apply in the Silurian in general: *the more abundant the fishes, the fewer the marine invertebrates*, and vice versa. Zones K_2 and K_3 are typically marine, and fish are found rarely and only in fragmentary form; in K_4 invertebrates and fish are both abundant but are not found in the same layers; in K_1 fish (and eurypterids) are abundant and well preserved, while marine invertebrates are rare.

With regard to the scale and spine findings of Zones K_2–K_4, we have a situation comparable to that of the roughly contemporaneous Beyrichienkalk and the Scanian scale-bearing beds farther west in the Baltic. The fragmentary nature of the remains might be attributed to the work of scavengers if these fishes are considered marine or to disintegration during transportation from stream mouths if they are believed to be of fresh water origin. On the whole, however, consideration of the Oesel situation in its entirety seems to me to throw the balance rather strongly towards fresh water origin for these scales and spines.

The critical problem is that of Zone K_1, with its abundant and well-preserved fauna. The assemblage here of fishes, eurypterids and ceratiocarids is one which we have seen repeatedly in Silurian and early Devonian localities which are clearly of fresh water nature, and O'CONNELL would have it that we are dealing here with a fluviatile deposit. I fail to be convinced that this is the case. The conditions of deposition suggest quiet waters, and the presence of at least a few definitely marine invertebrates strongly indicates that, for the beds as a whole, the region certainly lay no farther inland than could be reached by salt tidal waters.

On the other hand, claims that the eurypterid-fish beds are typically marine seem no better founded. The marine invertebrates reported are limited in variety and very limited in numbers and there is no published evidence, as far as I am aware, that they are closely associated with the eurypterids and fishes. Resort may be had to the supposition that the fauna was originally a typically marine one, and that diagenetic processes have removed most of the invertebrates. There has been a process of solution of carbonate shells in at least certain instances in the K_1 Zone, but the known invertebrate forms are adequately identifiable from the moulds remaining; considering the long series of students of these beds, had a richer marine fauna been present, indications of it would surely have been discovered and described. Here, as in other instances, I find myself sceptical—reasonably, I think—of hypotheses which propose diagenetic disappearance of marine invertebrates exclusively in those beds of a series which carry fish.

On the whole, the evidence suggests that the eurypterid-fish beds of K_1 are deposits laid down in lagoons in which *on the average* the water was of low salinity. With this much, I think most students of the subject would agree. From this point onwards advocates of fresh- or salt-water fish origins may reasonably disagree. (1) It may be assumed by those who favour marine origins that the lagoonal conditions were uniformily brackish during the time of deposition of the K_1 beds and that the fishes were marine forms but euryhaline, tolerant enough of brackish conditions to exist here as well as in a normal marine environment. (2) Again assuming uniformity of brackish conditions, fresh water advocates may argue that the fishes of the time were normally inland dwellers but sufficiently euryhaline to descend to brackish waters. (3) A third possibility is that the lagoons were deltaic and fluctuated from time to time in salinity, with the fauna shifting from time to time between one of fish and eurypterids when the waters were relatively fresh, and one with sparse invertebrates replacing them when the salt content increased.

All three assumptions are equally reasonable as far as the evidence from Oesel alone is concerned. I am strongly disinclined to accept the first hypothesis and tend to favour the second, and more especially the third; this not alone because of my admitted prejudice, but particularly because the complete lack, as we have seen, of any comparable fauna of fish of this age in any typical marine bed.

CONCLUSIONS

I have above reviewed all fish occurrences from the European Silurian (and Downtonian) cited by GROSS; these include all described pre-Devonian vertebrate finds except for those from the relatively few American continental localities previously studied and a few scattered European finds omitted by GROSS or described too late to be included in his review. They may be grouped under the following headings:

(1) From typical marine deposits (as in England, Podolia, Bohemia) a very few rare and generally fragmentary remains, mainly scales or spines, which may most reasonably be regarded as strays.

(2) Finds in beds of Downtonian or " Old Red " facies of transitional or continental type, as in Great Britain, Norway, Podolia, Bohemia and Pas-de-Calais.

(3) Isolated scales and spines from late Silurian Baltic deposits (as the Beyrichienkalk, Scania, Zones K_2–K_4 of Oesel) which are of somewhat questionable nature but on the whole reasonably interpreted as materials drifted out from the advancing shore-line.

(4) The Oesel K_1 fauna of eurypterids and fish, which in itself can be used as an argument for either fresh- or salt-water origins, but when viewed in the light of the whole picture is most reasonably interpreted on the hypothesis of continental origins.

In sum, the European record is in entire agreement with the thesis that the primary home of the vertebrates in Silurian times lay in fresh waters, and adds confirmatory evidence to the proof of fresh water vertebrate origins given by study of kidney structure and function. It is not at all improbable that evidence may be forthcoming that some vertebrates at least were euryhaline or even definitely marine in habitus as early as the Silurian. But unless or until a very considerable body of data of this sort—now lacking—be accumulated, I see no reason for serious consideration of a marine history for the early vertebrates. As I have said on an earlier occasion, " A consideration of selected portions of the evidence might permit of such an interpretation; but examination of the entire body of facts . . . leads unmistakably to the conclusion that the early vertebrates were dwellers in fresh water."

REFERENCES

Amsden, T. W. (1955), Lithofacies map of Lower Silurian deposits in central and eastern United States and Canada. *Bull. Amer. Assoc. Petrol. Geol.*, **39** (1), 60–74.

Born, A. (1926), Das Gotlandium. *In* Salomon, W. *Grundzüge der Geologie*, **2**, 143–193.

Bouček, B. (1934), Bemerkungen zur Stratigraphie des böhmischen Gotlandien und seinen Faziesverhältnissen. *Centralbl. f. Mineral.*, 1934, 477–494.

Brotzen, F. (1933 a), Die silurischen und devonischen Fischvorkommen in Westpodolien. *Palaeobiologica*, **5**, 423–466.

Brotzen, F. (1933 b), Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. *Zeitschr. f. Geschiebeforschung*, **9**, 55–63.

Brotzen, F. (1936), Beiträge zur Vertebratenfauna des westpodolischen Silurs und Devons. I. *Protaspis arnelli* n.sp. und *Brachipteraspis* n.gen. *latissima* Zych. *Arkiv f. Zool.*, **28A** (22), 1–52.

Chamberlin, T. C. (1900), On the habitat of the early vertebrates. *Jour. Geol.*, **8** (5), 400–412.

Gross, W. (1933), Die phylogenetische Bedeutung der altpaläozoischen Agnathen und Fische. *Palaeont. Zeitschr.*, **15**, 102–137.

Gross, W. (1947), Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica*, **96A**, 91–158.

Gross, W. (1950), Die paläontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoischen Schichten. *Abh. deutsch. Akad. Wiss. Berlin, Math.-natur. Kl.*, 1949 (1), 1–127.

Heintz, A. (1939), Cephalaspida from Downtonian of Norway. *Norske Vidensk. Akad. Oslo Skr.* 1, *Mat.-Naturw. Kl.*, 1939 (5), 1–119.

Hoppe, K.-H. (1931), Die Coelolepiden und Acanthodier des Obersilurs der Insel Ösel. Ihre Paläobiologie und Paläontologie. *Palaeontographica*, **76**, 35–94.

Jones, O. T. (1929), Silurian system. *In:* Evans, J. W. and Stubblefield, C. J., *Handbook of the geology of Great Britain*, pp. 88–127. London.

Kettner, R. and Kodym, O. (1919), Nová stratigraphie Barrandienu. *Cas. Nár. Musea*, **93**, 48–59.

Kiaer, J. (1908), Das Obersilur im Kristianiagebiete. *Skr. Vidensk.-Sels. Christ.*, 1, *Math.-naturv. Kl.*, 1906 b (2), 1–595.

Kiaer, J. (1924), The Downtonian fauna of Norway. I. Anaspida with a geological introduction. *Vidensk. Skr. I. Mat.-naturv. Kl.*, 1924 (6), 1–139.

King, W. W. (1934), The Downtonian and Dittonian strata of Great Britain and north-western Europe. *Quart. J. Geol. Soc. London*, **90**, 526–570.

Kozlowski, R. (1929), Les Brachiopodes gothlandiens de la Podolie Polonaise. *Palaeont. Polonica*, **1**, 1–254.

Krause, A. (1877), Die Fauna der sogen. Beyrichien- oder Choneten-Kalke des norddeutschen Diluviums. *Zeits. deutsch. geol. Ges.*, **29**, 1–49.

Lehman, J.-P. (1937), Les Poissons du Downtonien de la Scanie (Suède). Rennes. (*Thèse, Faculté des Sciences de l'Université de Paris.*) 98 pp.

Leriche, M. (1906), Contribution a l'étude des poissons fossiles du Nord de la France et des régions voisines. *Mém. Soc. Géol. Nord*, **5**, 1–430.

MacFarlane, J. M. (1923), *The evolution and distribution of fishes*. New York. 564 pp.

Moore, R. C. (1933), *Historical geology*. New York. 673 pp.

O'Connell, M. (1916), The habitat of the Eurypterida. *Bull. Buffalo Soc. Nat. Sci.*, **11** (3), 1–277.

Perner, J. (1918 a), Vorläufiger Bericht über die Fischfauna des böhmischen Obersilur und die Fossilen verteilung in den F_1-Schichten. *Centralbl. f. Mineral.*, 1918, 318–322.

PERNER, J. (1918 B), O rybách z pásma Ff_1 (Lochkovské vápence) a vertikálním rozšíření zkamenělin v těchto vrstvách. *Cas. Nár. Musea Cesk.*, **92,** 72–76.

PERNER, J. and KODYM, O. (1919), O rozclenení svrchního siluru v Cechách. *Cas. Nár. Musea Cesk.*, **93,** 3–19.

PERNER, J. and KODYM, O. (1922), On the zonal division and correlation of the Silurian of Bohemia. *Amer. Jour. Sci.*, (5) **4,** 53–72.

POMPECKJ, J. F. (1923), Gigantostraca und Scorpionida. *Palaeont. Zeitschr.*, **5,** 319–338.

PRANTL, F. and PŘIBYL, A. (1948), Revision of the Bohemian Silurian Eurypterida. *Rozpravy Stát. Geol. Ústavu Ceskoslov. Rep.*, **10,** 60–116.

ROEMER, F. (1885), Lethae erratica. *Palaeont. Abh.*, **2** (5), 1–173.

ROMER, A. S. (1933), Eurypterid influence on vertebrate history. *Science*, (n.s.) **78,** 114–117.

ROMER, A. S. (1955), *The Vertebrate Body*. 2nd ed., Philadelphia. 644 pp.

ROMER, A. S. and GROVE, B. H. (1935), Environment of the early vertebrates. *Amer. Midl. Natur.*, **16** (6), 805–862.

RUEDEMANN, R. (1934), Eurypterids in graptolite shales. *Bull. New York State Mus.*, **27,** 374–385.

SAMSONOWICZ, J. (1950), The Devonian in Volhynia. *Acta Geol. Polonica*, **1,** 401–518.

SMITH, H. W. (1932), Water regulation and its evolution in the fishes. *Quart. Rev. Biol.*, **7,** 1–26.

SMITH, H. W. (1936), The retention and physiological role of urea in the Elasmobranchii. *Biol. Rev.*, **11,** 49–82.

SMITH, H. W. (1953), *From Fish to Philosopher*. Boston. 264 pp.

STENSIÖ, E. A. (1944), Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of western Podolia. II. Notes on two arthrodires from the Downtonian of Podolia. *Arkiv f. Zool.*, **35A** (9), 1–83.

STØRMER, L. (1934), Merostomata from the Downtonian sandstone of Ringerike. *Norsk Vid.-Akad. Skr. I, Mat.-Naturv. Kl.*, 1933 (10), 1–125.

STØRMER, L. (1935), *Dictyocaris*, Salter, a large crustacean from the Upper Silurian and Downtonian. *Norsk Geol. Tidsskr.*, **14,** 267–298.

VERSLUYS, J. (1923), Die Abstammung und Differenzierung der Gigantostraken. *Palaeont. Zeits.*, **5,** 292–319.

WESTOLL, S. J. (1945), A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms. *Trans. Roy. Soc. Edinburgh*, **61,** 341–357.

ZYCH, W. (1927), Old-red de la Podolie. *Trav. Serv. Géol. Pologne*, **2,** 1–65.

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The production of antibiotics by plankton algae and its effect upon bacterial activities in the sea *

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Summary—Laboratory experiments with *Chlorella* and plankton diatoms show that small concentrations of the algae produce antibiotics which highly decrease the bacterial activities, including respiration. If the concentration of organic matter is about the same as in natural sea water, the decrease in bacterial respiration is of a much higher order of magnitude than the rate of photosynthesis of the algae.

The normal light and dark bottle oxygen experiments cannot be used for measuring organic productivity in oligotrophic water. Intense bacterial activities, which occur in the dark bottles as soon as natural sea water is enclosed in the bottles, are much reduced in the light bottles; thus there is an important difference in oxygen consumption between the two kinds of bottles, a difference which has nothing to do with photosynthesis. The disagreement for tropical oceanic water between the oxygen technique and the C-14 technique is thus easy to explain.

It is suggested that the average age of the dissolved organic matter found in sea water is some thousand years. This organic matter is most likely the most important food source—although indirectly—for the bottom animals living at very great depths.

INTRODUCTION

In productive coastal areas the so called " light and dark bottle " oxygen experiments originally introduced by Gaarder and Gran (1927) have been of great value for estimating organic productivity by the phytoplankton. Riley (1939), however, published results of such experiments lasting 3 days from the Sargasso Sea, which according to all evidence is one of the regions in the oceans most scarce in organic life. According to Riley's measurements, this sea would be one of the most productive sea areas of the world—if not the most productive.

Steemann Nielsen (1954), by using the carbon-14 method, could not verify the high rate of organic production in the Sargasso Sea. On the contrary, this sea was found to be about the poorest area in all oceans regarding organic productions by the plankton algae. This result, on the other hand, is in absolute agreement with the general hydrographic conditions (minimum supply of nutrient salts), the low standing crop of phyto- and zooplankton found, and the scarcity of fish. It could further be shown that, theoretically, an organic production of the size claimed by Riley must be considered impossible in the clear water of the Sargasso Sea, where most light by far is absorbed by the water itself. The energy absorbed by the plankton algae is only sufficient for a small photosynthetic rate.

It could, however, be verified that the light and dark bottle oxygen experiments give results comparable with those obtained by Riley.

It is a well-known fact (cf. the next section) that the bacterial activities in sea water are highly intensified if the water is enclosed in glass bottles. The respiration rates found by using light and dark bottle experiments of long duration in tropical oceanic water must be considered almost entirely due to the increased bacterial activities. They do not tell anything about the rate of respiration under natural conditions in the sea. The smaller oxygen consumption in the light bottles as compared with the dark bottles (no oxygen production is ever observed) might of course be due to photosynthesis. A reduction of the bacterial respiration directly or indirectly due to light can, however, as well explain the fact. Originally (STEEMANN NIELSEN, 1952) the idea of a direct bactericidal effect of sunlight was suggested. In the 1954 article it was, however, suggested instead that antibiotics produced by the plankton algae in light reduce the bacterial activity. It was shown first by PRATT *et al.* (1944) that antibiotics are produced by plankton algae.

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RYTHER (1954) suggests that the disagreement between the light and dark bottle technique and the 14C technique in tropical oceanic water is possibly due to (1) the supposition that plankton algae nearly exclusively respire the newly formed products of their photosynthesis and (2) the supposition that the rate of algae respiration is about equal to the photosynthetic rate in these waters.

Experiments presented by RYTHER in order to give his suggestions an experimental background have now been repeated in this laboratory (STEEMANN NIELSEN and AL KHOLY, in press). No corroboration of his results could, however, be obtained. These seem obviously to be the result of an unsatisfactory experimental technique. It is further shown that his suggestions would lead to some fantastic and quite unrealistic assumptions of what is going on in the oceans.

RYTHER'S suggestion that the algae nearly exclusively respire the newly formed products of their photosynthesis seems to be contradicted by the work of the Berkeley Group. According to CALVIN and MASSINI (1952), algae in light respire, to a slight degree only, newly formed products. There is, however, as will be shown in a subsequent paper, really a connection between photosynthesis and respiration, although not of the extent supposed by RYTHER. It has some influence on the measurement of the organic production by the 14C technique. Under very unfortunate conditions in nature the results from using this technique may possibly be up to about 15% too low. Normally, however, the influence is negligible.

DISSOLVED ORGANIC MATTER IN SEA WATER AND ITS DECOMPOSITION

One of the most amazing statements about the sea is that by far the largest amount of the organic matter existing anywhere on this globe is found dissolved in the oceans. According to KEYS, CHRISTENSEN and KROGH (1935) the dissolved organic matter in water from all depths of the oceans corresponds to about 1·2–2·0 mg C and 0·2 mg N per litre. About 15 kg organic matter is thus found below every m^2 ocean surface. In comparison, the average annual net production per m^2 by the phytoplankton is only about 1% of this (STEEMANN NIELSEN, 1952).

Most of the organic matter produced by the plankton algae is presumably used rather soon for respiration in some organism or other. The magnitude of animal life in the sea could otherwise scarcely be explained. The organic matter dissolved in ocean water must therefore on an average be rather old, presumably several thousand years.

The nature of the organic matter in question has not yet been investigated. If the water is *in situ*, an extremely slow decomposition of the organic matter takes place. About 25–50% is, however, readily decomposed by bacteria, if the water is stored in glass bottles (KEYS, CHRISTENSEN and KROGH, 1935; WAKSMAN and CAREY, 1935).

It has been shown by ZOBELL and ANDERSON (1936) that the presence of solid surfaces is the factor which makes the bacterial decomposition of dissolved organic matter in ocean water possible. Small bottles in which the ratio—inner surface of the bottle : volume of the water—is high, give rise to a faster bacterial decomposition than bigger bottles, in which the ratio is lower. The addition of glass beads in the same way increases the bacterial activity. According to ZoBELL (1946) the influence of the surfaces may be explained (1) through accumulation of the organic matter due to surface activities, (2) by assuming that exoenzymes necessary for attacking the organic matter can only be maintained in sufficient concentration if solid surfaces are present.

In natural sea water, solid surfaces are of course found. The phytoplankton, zooplankton, and particulate dead material all have solid surfaces. In oceanic surface water these surfaces are, however, scarcely more than about 10 mm^2 per litre. In water from deeper layers they are much smaller. The inner surface of a one-litre bottle is about 10^5 as large.

The surfaces of plankton algae seem normally to be rather unsuitable for bacterial growth. If plankton algae are growing well, very few bacteria—if any—can be observed to be attached to their surfaces. If the surfaces of the algae are densely covered with bacteria, this indicates that they are not in a healthy state. The whole procedure of growing algae in a pilot plant, where it is impossible to keep the culture sterile, is based upon the fact that the culture itself is able to keep the bacterial activities at a minimum. This has been known for a long time. Thus WAKSMAN *et al.* (1937) state that " The result . . . confirmed the previous observation that, in the presence of a living culture of *Nitzschia* (a plankton algae), the bacterial activities were very limited."

The statement above does not contradict the fact, often observed, that bacteria mostly are more abundant where a high phytoplankton population is found (e.g. GRAN, 1933). The heterotrophic micro-organisms are first of all numerous at the end of a phytoplankton bloom. Beside bacteria, heterotrophic flagellates are also found. Due to the bloom of autotrophic organisms, relatively large quantities of easily accessible organic matter first of all originating from dying and half-digested cells, are contributed to the water. Solid surfaces apparently are not necessary for the bacteria attacking this easily accessible organic matter (no exoenzymes necessary?). They can thus also be in a real planktonic state.

It can be stated that the dissolved organic matter in sea water consists of the following components:

> (1) matter very easily accessible for bacteria, (2) matter only accessible for bacteria if solid surfaces are present, (3) matter which apparently cannot be decomposed by bacteria at all. In oligotrophic oceanic water, practically only the two last-mentioned components are found.

If the hypothesis about the importance of solid surfaces for the bacteria to attack the normal stock of " old " organic matter is correct, a dense bacterial flora should always be found on the surface of plankton algae. As such a flora normally is not found, the algae must be able to prevent the development.

PRATT *et al.* (1944) showed that the plankton alga *Chlorella* produces antibiotics with a high effect on bacterial growth. The normal absence of bacteria in any amount from the surfaces of healthy plankton algae of all kinds indicates that all these species produce antibiotics. The ability to avoid bacterial settlement to any higher degree by producing antibiotics may be considered to be a rather important condition, the lack of which would make these species fairly unsuitable for aquatic life.

As mentioned above, Pratt *et al.* (1944) showed that the antibiotics are given off by the alga to the water. In a sample of natural sea water containing phytoplankton, it must therefore be expected that the antibiotics produced are not only effective for the prevention of bacterial growth on the surface of the algae themselves, but also on other surfaces, thus on the inner walls of the experimental bottles.

EXPERIMENTS

Photosynthesis may be written $CO_2 + H_2O \rightarrow (H_2CO) + O_2$; respiration may be written $(H_2CO) + O_2 \rightarrow CO_2 + H_2O$. Respiration by the plankton algae, and by all other organisms present, is going on both in the light and the dark, photosynthesis by the plankton algae is going on only in the light.

When making experiments in which the amount of dissolved oxygen in the water is measured before the experiment, and in light and dark bottles at the end of the experiment, the difference in the O_2 content between the initial bottles and the dark bottles represents the rate of respiration by all organisms. The rate of photosynthesis should be measured by the O_2-difference in the light and in the dark bottles. A necessary condition is, however, that light neither directly nor indirectly decreases the rate of respiration, a condition which is not fulfilled.

Experiments were made in which bacteria were growing together with very few algae (the freshwater green alga, *Chlorella pyrenoidosa* or the marine diatom, *Thalassiosira nana*). The rate of photosynthesis per number of cells was first measured in a special experiment using a sufficient concentration of the algae. The method was the same as used in the main experiment. There the concentration of the algae was made so low that it would have been impossible to measure the rate of photosynthesis by the O_2-production according to the normal Winkler technique. By counting the number of algae cells at the start and at the end it was possible to determine growth during the experiments, and thus the total rate of photosynthesis.

In the experiments with the marine diatom, sea water from the Sound enriched with some nutrient salts was employed. In the *Chlorella* experiments the culture solution D (Österlind, 1949) was used in a slightly modified form. In both cases 7–8 mg glucose and 2–4 mg peptone was added per l. The light intensity was 8,000 lux, the temperature 22 C. In every experiment 3 bottles of each kind was employed. Two Winkler titrations were made with water from each bottle.

In order to get an incubation by bacteria, the culture solution used for the main experiments was incubated with 0·5 ml/litre of freshly collected surface water either from a lake near Woods Hole (*Chlorella* experiments) or from the Sound (the marine diatom). The water was filtered through a coarse paper filter before use.

In Table 1 is given a typical experiment.

Table I. Chlorella pyrenoidosa

Rate of photosynthesis (real assimilation) in preliminary experiment 1·46 0·01 ml O_2 l per hour.

Dilution of the algae used in the main experiment 1 : 10·000.

Duration of main experiment 72 hours—3 light periods (44 hours together) alternating with 3 dark periods.

Rate of photosynthesis (real assimilation) by *Chlorella* in light bottles (corrected for growth) per 72 hours 0·04 ml $0_2/1$.

O_2-consumption in dark bottles per 72 hours 3·59 ± 0·02 ml. $O_2/1$.

O_2-consumption in light bottles per 72 hours 2·92 ± 0·03 ml $O_2/1$.

Reduction in O_2-consumption in light bottles as compared with dark bottles 0·67 ± 0·04 ml O_2 l.

It is thus evident that the difference between the light and the dark bottles is not due to *Chlorella* photosynthesis. In a corresponding series made simultaneously but without *Chlorella* added the O_2 consumption was the same in the light and in the dark bottles. The difference was 0·03 ± 0·08. This indicates that no photosynthesizing cells in any important number were introduced together with the bacteria. It further shows that light has no direct effect on the activity of the bacteria developing in the bottles. This is in accordance with the results published by VACCARO and RYTHER (1954).

There is no reason to give any details about the other similar experiments made, using either *Chlorella* or the marine diatom. The results are similar. The difference in oxygen consumption between light and dark bottles was between 12 and 30 times higher than the oxygen production due to the photosynthesis of the algae.

It turned out to be impossible in these experiments to use unsterilized, stored sea water. Products produced by the special bacterial flora developing made the use of Winkler titrations rather impossible. The water was therefore collected immediately before an experiment.

Experiments were made to investigate the influence of an addition of a substratum from which a rather dense, vigorously growing *Chlorella* population had been filtered off. Although a pronounced influence was found, the direct influence of a dilute *Chlorella* population was pronouncedly higher. By adding 4% of such a substratum at the start of an experiment lasting 2 days, only a decrease in O_2-consumption of 0·09 ml/l was found. In the corresponding experiment the influence of a very dilute *Chlorella* population in the light bottles was 5 times as high. This is, however, in perfect agreement with the statements by PRATT (1948) according to which the concentration of the antobiotics produced by algae seems to be higher at a low concentration of growing *Chlorella* than at a higher concentration.

The experiments presented in this article show that the presence of algae, presumably due to the production of antibiotics, effects a reduction in the O_2-consumption of the bacteria in the light bottles. This reduction was of a higher order of magnitude than the O_2-production due to the photosynthesis of the algae. There is no reason to believe that the plankton algae living in oligotrophic oceanic water should not behave in just the same way. Thus it is not possible to use the light and dark bottle oxygen technique here. In eutrophic areas the technique is fully applicable.

In the culture medium used in the present experiments the organic matter present was easily accessible for the decomposing bacteria. It must be assumed that a number of different species took part in this decomposition. In oceanic water the dissolved organic matter presumably is only accessible for some few bacterium species able to excrete the necessary exoenzymes. It is therefore rather probable that the effect of the antibiotics produced can be still higher here. In the experiment shown in Table 1, oxygen consumption was reduced by 19% in the light bottles. In light and dark bottle experiments in oligotrophic oceanic water the reduction is mostly more than 50%.

DISCUSSION

By looking at a series of light and dark bottle experiments made in the open ocean, it is evident that the rate of respiration in the dark bottles varies from one station to another. Thus the values published by RILEY (1939) for 3 days' experiments with surface water from the Sargasso Sea varies from 0·12 to 0·51 ml O_2 consumed per l. There is no reason to believe that the content of organic matter in the surface water of this rather uniform sea should vary much from place to place. It is more likely that the amount of antibiotics present in the water at the time it is collected varies somewhat from place to place. The time of the day for the collection may be rather important, too. Near sunset the concentration of antibiotics is possibly higher than near sunrise.

It is at present impossible to state if non-autotrophic organisms independent of light secrete antibiotics. This is by no means unbelievable. Some observations on the *Galathea* expedition support this possibility. A verification is, however, needed.

KROGH (1934)—as he explained it himself—offered a vague suggestion that the animal life at great depths in the oceans depends on bacteria. At that time he knew the concentration of soluble organic matter in ocean water. He knew, too, that this organic matter normally was not decomposed by bacteria. He did not, however, know that a material part of this organic matter is easily decomposed if solid surfaces are present. At the sea bottom such solid surfaces are present. A rather considerable decomposition of this organic matter is apparently going on here constantly. Most of the " old " organic matter diluted in sea water is most likely ultimately decomposed at the sea bottom. The bacteria living on this matter present most likely a very important, although not the only food source for the bottom animals at very great depths.

REFERENCES

CALVIN, M., and MASSINI, P. (1952), The path of carbon in photosynthesis. (XX. The steady state.) *Experientia* **8,** 445–457.

GAARDER, T., and GRAN, H. H. (1927), Investigation of the production of plankton in the Oslo Fjord. *Rapp. Proc. Verb. Cons. Perm. Int. Expl. Mer,* **42,** 3–48.

GRAN, H. H. (1933), Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of phytoplankton in August, 1932. *Biol. Bull.,* **64,** 159–182.

KEYS, A., CHRISTENSEN, E. H., and KROGH, A. (1935), The organic metabolism of sea water with special reference to the ultimate food cycle in the sea. *J. Mar. Biol. Assoc., U.K.,* **29,** 181–196.

KROGH, A. (1934), Conditions of life at great depths in the ocean. *Ecol. Monogr.,* **4,** 430–439.

ÖSTERLIND, S. (1949), Growth condition of the alga *Scenedesmus quadricauda,* with special reference to the inorganic carbon sources. *Symbolae Botanicae Upsaliensis,* **10** (3), 1–141.

PRATT, R., DANIELS, T. C., EILER, J. J., GUNNISON, J. B., KUMLER, W. D., ONETO, J. F., and STRAIT, L. A. (1944), Chlorellin, an antibacterial substance from *Chlorella. Science,* **99,** 351–352.

PRATT, ROBERTSON (1948), Studies on *Chlorella vulgaris.* XI. Relation between surface tension and accumulation of chlorellin. *Amer. J. Bot.,* **35,** 634–637.

RILEY, G. A. (1939), Plankton studies. II. The western North Atlantic, May–June, 1939. *J. Mar. Res.,* **2,** 145–162.

RYTHER, J. H. (1954), The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. *Deep-Sea Res.,* **2,** 134–139.

RYTHER, J. H., and VACCARO, R. F. (1954), A comparison of the oxygen and ^{14}C methods of measuring marine photosynthesis. *J. du Cons.,* **20,** 25–34.

STEEMANN NIELSEN, E. (1952), The use of radio-active carbon (^{14}C) for measuring organic production in the sea. *J. du Cons.,* **18,** 117–140.

VACCARO, R. F., and RYTHER, J. H. (1954), The bactericidal effects of sunlight in relation to " light " and " dark " bottle photosynthesis experiments. *J. du Cons.,* **20,** 18–24.

WAKSMAN, S. A., and CAREY, C. L. (1935), Decomposition of organic matter in sea water by bacteria. *J. Bacteriol.,* **29,** 531–543.

WAKSMAN, S. A., STOKES, J., and BUTLER, M. R. (1937), Relation of bacteria to diatoms in sea water. *J. Mar. Biol. Assoc., U.K.,* **22,** 359–373.

ZOBELL, C. E. (1946), *Marine microbiology.* Waltham, Mass., Chronica Botanica Co., 240 pp.

ZOBELL, C. E., and ANDERSON, D. Q. (1936), Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces. *Biol. Bull.* **71,** 324–342.

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On the nature and action of coelenterate toxins*

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Summary—Tetramethylammonium, known to occur in sea anemones, has been thought to be one of constituents of coelenterate nematocyst toxins. To test this suggestion it was first shown that the tendency to drop legs, or autotomize, in the fiddler crab *Uca mordax*, was reduced by previous injection of extracts of tentacles of two species of anemones and of *Physalia*, the Portuguese-man-of-war. It was then found that injected tetramethylammonium chloride or acetylcholine had similar actions to those of the extracts.

Further experiments of a comparable nature were done at another location, using as a test animal the shore crab, *Hemigrapsus nudus*. Extracts of tentacles of *Metridium*, when injected into *H. nudus*, produced spontaneous autotomy of walking legs and chelae, followed by a degree of paralysis dependent upon the dose.

After the injection of tetramethylammonium chloride into *H. nudus* there were no spontaneous autotomies, but there was a type of paralysis similar to that produced by tentacle extracts.

Tetraethylammonium chloride, and a related compound called Banthine, were highly effective in blocking the autotomy-inducing and paralyzing actions of *Metridium* tentacle extracts. This is added evidence that a quaternary ammonium base similar to tetramethylammonium occurs in coelenterate tentacle extracts.

When *Metridium* and *Cyanea* tentacle extracts were tested on an isolated mollusc heart, evidence for the presence of an excitor amine was obtained. It appeared not to be histamine. Later experiments strongly suggested that the material with the marked action on the molluscan heart was 5-hydroxytryptamine, a known histamine-releaser and potent pain producer.

Through the use of paper chromatography further evidence has been obtained for the presence of 5-hydroxytryptamine in extracts of tentacles of *Metridium* and *Physalia*. This approach has also shown the presence of two or more quaternary ammonium bases, one of which has been tentatively identified as urocanylcholine, also known as murexine.

The pain producing factor in coelenterate tentacle extracts is probably 5-hydroxytryptamine; while paralysis could be due to two or more related quaternary ammonium bases such as tetramethylammonium and urocanylcholine.

The painful and paralyzing nature of the " sting " of certain jellyfishes and the siphonophore, *Physalia*, is well known. Less well known is the fact that all coelenterates possess stinging organelles, called nematocysts, which serve two main functions; one, defence, and two, immobilization of prey for ease in feeding. The latter is well illustrated by a hydra subduing and engulfing a large and active Daphnia. The ability to produce a painful sting is not an indication of the amount of toxic substance present in the tentacles of a given species; rather, it is the ability of the nematocysts to penetrate the skin. This ability varies greatly with species, and effective penetration of human skin is restricted to the nematocysts of relatively few species of coelenterates. For example, the sea anemone, *Anemonia sulcata*, has penetrants that enter the skin of the finger sufficiently to cause a stickiness between the tentacles and the skin, but seldom is there subsequent pain. However, when a tentacle of this species is placed on the tongue, a painful and long-lasting burning sensation results, indicating that

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the nematocysts have been able to penetrate the more delicate epithelium of the tongue.

Numerous attempts have been made to determine the nature of nematocyst toxins. Among the earlier studies were those of RICHET, which began in 1902 (for complete report see RICHET and PORTIER (1936)). He isolated two chemically unidentified substances which were named " thalassin " and " congestin ". Two papers summarizing much of the earlier work on nematocyst toxins are those of THIEL (1935) and SONDERHOFF (1936). Recently, BOISSEAU (1952) has used histochemical procedures in an attempt to identify the capsular contents of nematocysts.

Coelenterates feed to a considerable extent on crustaceans, and there are close commensal associations between coelenterates and crustaceans (e.g. the several hermit crab–sea anemone pairs). It is natural, therefore, that attention should have been paid to the physiological action of coelenterate extracts when injected into crustaceans. Many interesting observations of this sort have been made by CANTACUZÈNE (1925 A, B, 1926), CANTACUZÈNE and COSMOVICI (1925), CANTACUZÈNE and DAMBOVICEANU (1934 A, B, C), COSMOVICI (1925 A, B, C, D, E), REY (1940), MANUTA (1943) and others. It is clear that extracts of coelenterate tentacles (the chief nematocyst-bearing structures) have a powerful paralyzing action on crustaceans; also, that a crustacean which lives in close association with a coelenterate develops a resistance to the paralyzing factor(s).

This paper will summarize a series of observations on the chemical nature and physiological actions of nematocyst toxins. The studies were begun in 1950 and were subsequently carried on as part of a larger study on invertebrate pharmacology. Various localities have provided abundant experimental material, and different portions of the work have been carried out at the Lerner Marine Laboratory, Bimini, British West Indies; the Marine Field Laboratories of the University of Washington, Friday Harbor, Washington; the Plymouth Laboratory, Plymouth, England; and the Bermuda Biological Station. I am indebted to the Directors and Staffs of these Marine Stations for the excellent facilities that have been provided. Work toward the identification of the active materials, mainly by use of paper chromatography, has been done at Harvard University. Because the work at each laboratory was carried out on local representatives, it cannot readily be integrated. It seems best therefore, to give a brief account of the findings made at each location.

In view of Professor BIGELOW's interest in the coelenterates, and especially the scyphomedusae, it is not unfitting that a discussion of nematocyst toxins be included in this volume. It is a privilege to dedicate this paper to one from whom I have learned so much.

I. OBSERVATIONS MADE AT BIMINI (MARCH 27–APRIL 7, 1950)

The earliest observations in this series were made at Bimini, and concerned mainly the effect of tentacle extracts and certain selected chemicals on the autotomy reflex of a species of fiddler crab. WELSH and HASKIN (1939) had found the frequency of dropping of legs in certain crustaceans to be a sensitive indicator of the activity of injected substances, such as acetylcholine and adrenaline. On the assumption that nematocyst substance might act on some step in conduction or transmission of nerve impulses, the autotomy reflex was chosen as an indicator of such action.

Preliminary tests of three species of fiddler crabs found on North Bimini (*Uca* *heterochelos* (Lamarck), *U. leptodactyla* Rathbun and *U. mordax* (Smith))* showed *U. mordax* to be most suitable. In all experiments to be reported here, this species was used.

Tentacle extracts were prepared from *Physalia*, the Portuguese-man-of-war, and from two common sea anemones, *Condylactis gigantea* and *Aiptasia sp.* The extracts were prepared by grinding a known volume of tentacles with an equivalent volume of sea water, either with or without the addition of enough hydrochloric acid to make the suspension weakly acid to litmus paper. If necessary, after filtration the pH was adjusted with $NaHCO_3$ until the solution was neutral. Extracts were diluted as indicated, and injected at the base of one of the last pair of walking legs in amounts varying from 0·02 ml to 0·05 ml depending on the size of the crab. Crabs were injected in lots of five, and after 5–10 minutes the walking legs were grasped firmly with forceps for one or two seconds while the crab was held in a fixed position. This was usually a sufficient stimulus to produce autotomy in an untreated crab. Legs were grasped in a random order (cf. WELSH and HASKIN, 1939) and a record made of the number of autotomies in each crab. For each test the number of legs autotomized appears as the numerator of a fraction with a constant denominator of 40, this being the total number of walking legs possessed by 5 crabs.

Uninjected *U. mordax*, stimulated in the manner indicated, autotomized nearly all of their walking legs. Two lots of 5 males each dropped 36 of 40 legs. One lot of females dropped 37 of 40 legs. Two lots of males injected with 0·05 ml of sea water dropped 37 of 40 and 39 of 40 legs.

Table I shows the effects of extracts of three different species on the tendency to autotomize. It will be seen that the higher concentrations reduced the tendency to autotomize and even prevented any significant number of autotomies at the highest concentration used. The presence of a paralyzing agent in the extracts would account for such results.

Table I

Effects of several dilutions of tentacle extracts on the autotomy reflex in Uca mordax

Species	*No dilution*	1:10	1:100	1:1000	1:10,000
Physalia	0/40	5/40	23/40	40/40	
Aiptasia	0/40	7/40	40/40		
Condylactis		0/40	9/40	14/40	36/40

The reason for the great effectiveness of the extract of tentacles of the sea anemone, *Condylactis*, is not entirely clear. This anemone may actually carry a larger amount of paralyzing substance than *Physalia*, in a given weight of tentacle, but the ground tentacles used in making this extract stood for a longer period before filtering than in other extractions. This may have released more active material into solution.

Since *U. mordax* had responded to the extracts by showing clear signs of paralysis and by a reduced tendency to autotomize their appendages, they were obviously suitable for further study of possible paralyzing agents. The first to be tried was tetramethylammonium chloride (Me_4N) for the following reasons: (1) it is a normal constituent of coelenterates (ACKERMAN, HOLTZ and REINWEIN, 1923, and the hydroxide was named tetramine by these workers); (2) it has long been known to have curare-like properties in the vertebrates; and (3) there were earlier indications that it caused paralysis in insects and crustaceans (WELSH, unpublished).

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* Kindly identified by Dr. FENNER A. CHACE of the National Museum, Washington, D.C.

Tetramethylammonium chloride was dissolved in sea water and appropriate dilutions were made such that various amounts could be introduced by injection of a constant volume of fluid. After injection, legs were tested in the manner described for extracts. The results of two series of tests are given in Table II. It is clear that Me_4N is a moderately effective inhibitor of autotomy in *U. mordax*.

Since a tetraethylammonium salt (Et_4N) often has an action opposing that of Me_4N (e.g. WELSH and TAUB, 1950), this was injected in amounts of 0·5 mg and 0·05 mg. At the lower concentration the frequency of autotomy was 36/40, 39/40 and 40/40 in three experiments. After Et_4N, legs autotomized with remarkable ease.

Table II

Effect of several concentrations of tetramethylammonium chloride (Me_4N) on the autotomy reflex of Uca mordax

Me_4N	5 *mg*	0·5 *mg*	0·05 *mg*	0·005 *mg*
Series 1	0/40	11/40	30/40	38/40
Series 2	0/40	22/40	30/40	40/40

If acetylcholine is involved in the normal autotomy reflex in *U. mordax*, as it appears to be in *Petrolisthes* (WELSH and HASKIN, 1939), injected acetylcholine might facilitate autotomy or it might reduce it by raising the level to the inhibitory or paralytic range. With *U. mordax*, injected acetylcholine (0·5 mg/crab) reduced the frequency of autotomy. The triethyl analogue of acetylcholine (Et_3Ach) may antagonize acetylcholine (WELSH and TAUB, 1950). When 0·5 mg. of Et_3Ach was injected into *U. mordax*, legs autotomized with remarkable ease when grasped, and in each series there was 100 per cent autotomy. When Me_4N and Et_4N, or Ach and Et_3Ach, were injected simultaneously in 0·5 mg amounts, there was a significant antagonistic action between the pairs of compounds, and the tendency to drop legs was greater than with Me_4N or Ach injected alone.

Atropine, which blocks Ach at certain neuro-effector junctions, facilitated autotomy in *U. mordax*, when injected in a dose of 0·005 mg. Eserine, which prevents Ach from destruction by cholinesterase and therefore permits its accumulation, reduced autotomies to 31 of 40 at 0·001 mg and to 0 of 40 at 0·005 mg.

These results suggest that acetylcholine is involved in the autotomy reflex in *U. mordax*, and that any increase over normal body concentration results in some degree of paralysis. Me_4N, frequently shown to act like Ach in small amounts and to be paralytic in larger amounts, produces paralysis resembling that produced by the coelenterate extracts. Agents which may antagonize Ach and Me_4N, such as Et_3Ach and Et_4N, have actions on *U. mordax* which support the view that a methylated quaternary ammonium base might be a constituent of nematocyst toxins. There is yet no proof, however, that Me_4N (" tetramine "), although found in large amounts in coelenterates, is the paralyzing agent in nematocysts.

A further observation made in Bimini deserves to be reported. The sea anemone, *Aiptasia*, was often found in the Bimini lagoon, occupying an empty conch shell. Such shells frequently contained a single specimen of the red snapping shrimp, *Crangon armatus* (Rathbun).* Hermit crabs living in close association with sea anemones (especially *Eupagurus prideauxi*, which is nearly enclosed by the cloak anemone, *Adamsia palliata*) are known to be highly resistant to nematocyst toxins (CANTACUZÈNE, 1925 B; CANTACUZÈNE and DAMBOVICEANU, 1934 C; REY, 1940; MANUTA, 1943). To test for a possible acquired resistance of *C. armatus* to nematocyst toxins, appropriate doses of anemone tentacle extract were injected into several specimens. Three types of crustaceans were used as controls (*U. mordax*, *Callianassa sp.* and an unidentified shore crab). *Crangon armatus* survived for about 12 hours after injection with an amount of extract which, in less than one hour, killed the other crustaceans not found in association with sea anemones. This provides another example of the acquisition of a resistance to nematocyst toxins by a crustacean living in association with a sea anemone.

II. OBSERVATIONS MADE AT FRIDAY HARBOR (JULY 23, 1951, TO AUGUST 19, 1951)

(a) *Autotomy experiments*

At Friday Harbor, experiments similar to those done at Bimini were performed. As sources of toxins, the tentacles of the sea anemone, *Metridium dianthus*, and the large brown jellyfish, *Cyanea capillata*, were used. Tentacles were cut off and their volume determined. Hydrochloric acid was then added to pH 3–4. The tentacles were homogenized in a Waring blender and the homogenate strained through fine bolting silk. The pH of the liquid obtained was about pH 6. This extract was diluted with various proportions of sea water before use.

As a test animal the common shore crab of that region, *Hemigrapsus nudus*, was used. To compensate in part for a considerable size range, the crabs were sorted into two groups, those weighing about 2 to 4 gm and those weighing about 5 to 8 gm. Extracts and drugs were injected into the smaller crabs in a volume of 0·05 ml, while the volume used for the larger size was double this. Thus the amount of active material administered was, on the average, adjusted to body weight, since each test was done on a group of ten crabs.

Table III

Effect of extract of tentacles of Metridium dianthus *on autotomy in* Hemigrapsus nudus

Dilution	1:10	1:20	1:50	1:100	1:1,000
Total of walking legs autotomized	80/80	78/80	72/80	74/80	78/80
Spontaneous autotomies	42†	28	6	0	0

† A second extract at this dilution when tested on two lots of 10 crabs each gave 38 and 40 spontaneous autotomies.

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* Kindly identified by MR. JOHN C. ARMSTRONG.

Preliminary autotomy experiments soon showed that *H. nudus* differed significantly from *U. mordax*. The legs of *Hemigrapsus* usually had to be crushed with heavy forceps to induce autotomy and, after the injection of extracts or drugs, there was no graded response to be seen in the per cent of legs autotomized. However, it was noted that *Metridium* tentacle extract induced spontaneous autotomy of both chelae and walking legs, and the frequency of autotomy was related to dose. The results of a typical experiment are given in Table III. Such a table does not reveal the true nature of the response. In order to do this, the protocol of a typical experiment follows:

July 30, Metridium tentacle extract number 3 (=M-3)

4.25 p.m. Injected 10 *H. nudus* with 0·05 ml M-3, 1:1 with sea water.
4.30 p.m. 17 walking legs and 6 chelae had been spontaneously autotomized. Crabs are paralyzed and fail to right themselves when turned on their backs.
8.00 p.m. All crabs dead.

4.55 p.m. Injected 10 *H. nudus* with 0·05 ml of M-3, diluted 1:10 with sea water.
5.00 p.m. 18 walking legs and 10 chelae autotomized; crabs paralyzed.
8.00 p.m. All dead.

5.08 p.m. Injected 10 *H. nudus* with 0·05 ml of M-3, diluted 1:20 with sea water.
5.15 p.m. 30 walking legs and 11 chelae autotomized; crabs slightly paralyzed.
8.00 p.m. All apparently dead.

5.23 p.m. Injected 10 *H. nudus* with 0·05 ml of M-3, diluted 1:40 with sea water.
5.28 p.m. 21 walking legs and 8 chelae autotomized; crabs appear normal.
8.00 p.m. 3 crabs living but paralyzed.

5.35 p.m. Injected 10 *H. nudus* with 0·05 ml M-3 diluted 1:80 with sea water.
5.40 p.m. 6 walking legs and 2 chelae autotomized; crabs appear normal.
8.00 p.m. 3 crabs living but paralyzed.

5.45 p.m. Injected 10 *H. nudus* with 0·05 ml M-3 diluted 1:150.
5.50 p.m. 3 walking legs and 1 chela autotomized.
8.00 p.m. 9 crabs living but partly paralyzed; few can turn over when placed on backs.

When extracts of *Cyanea* tentacles were injected into *H. nudus*, spontaneous autotomies rarely occurred at any of the dilutions. With dilutions up to 1:50, paralysis occurred, but it was, if anything, less severe than with equivalent amounts of *Metridium* extract.

It will be recalled that tetramethylammonium chloride (Me_4N), like tentacle extracts, facilitated autotomy in *U. mordax*. When Me_4N was injected into *H. nudus*, even in high concentration, it seldom produced spontaneous autotomy, and reduced somewhat the tendency of stimulated legs to autotomize. While its paralyzing action resembled that of extracts of *Cyanea* tentacles, it appeared that *Metridium* extracts contained an active material other than an Me_4N-like component.

At Bimini it had been found that tetraethylammonium chloride (Et_4N) had an action opposite that of Me_4N and, likewise, that the actions of acetylcholine and its triethyl analogue (Et_3Ach) differed one from the other. Large doses of Et_4N could be injected into *H. nudus* with little effect. For example, 5 crabs were injected with 0·05 ml of 10% Et_4N. There were no spontaneous autotomies. In five minutes there were some twitching movements of the legs and the crabs were hyperexcitable, but twenty minutes after the injection they were normal in appearance and action.

If the spontaneous autotomies produced by extracts of *Metridium* tentacles were, in part, due to the presence of an Me_4N-like substance, it might be possible to prevent these autotomies by previous or simultaneous injections of Et_4N. Both procedures were followed. A given extract of *Metridium* tentacles (M-2), when diluted 1:10 with sea water, produced 38 spontaneous autotomies of chelae and walking legs, and produced a moderately severe paralysis. When this extract was diluted 1:10 with 1% Et_4N, rather than sea water, and 0·05 ml injected, there were *no spontaneous autotomies and no signs of paralysis.* In another experiment a given dilution of extract induced 40 spontaneous autotomies in ten crabs. In a second lot of crabs, 15 minutes after the injection of 0·05 ml of 1% Et_4N, the same dilution of extract produced no autotomies. Banthine, a drug used clinically to block acetylcholine action in vertebrate autonomic ganglia (as is Et_4N), is a derivative of Et_4N. In one experiment 0·05 ml of 10^{-3} Banthine completely blocked the autotomy-inducing and paralyzing action of a *Metridium* extract (M-3, 1:20) that had produced 50 spontaneous autotomies in a control group of 10 crabs.

These experiments done at Friday Harbor provided further evidence for the occurrence of a quaternary ammonium base (Me_4N derivative) in extracts of coelenterate tentacles. But Me_4N alone could not account for all of the observed actions of the extracts on the autotomy reflex of *Uca mordax* and *Hemigrapsus nudus*.

(b) *Evidence for an amine in tentacle extracts*

It is a common observation that the sting of *Physalia* and certain jellyfishes is followed by a painful burning sensation, localized swelling or wheals, redness and urticarial eruptions. Among the more recent descriptions of these and other symptoms, the following may be referred to for further details: ALLNUTT, 1926; WADE, 1928; FRACHTMAN and MCCOLLUM, 1945; MCNEILL, 1945; BERNSTEIN, 1947. These symptoms are among those that might be expected if histamine were a constituent of nematocyst toxins or if a histamine releaser were present. Accordingly, crabs were injected with histamine. A dose of 0·05 ml of 1% histamine caused marked paralysis but no spontaneous autotomies. One-tenth this dose caused a mild spastic stiffening of the legs. Pyribenzamine, an antihistamine, was tested. A dose of 0·05 ml of 1% pyribenzamine caused rapid autotomy of 70% of the chelae but no walking legs were dropped, nor could they be made to autotomize by crushing. One-tenth this dose of pyribenzamine clearly inhibited autotomy of legs and antagonized the autotomizing effect of *Metridium* tentacle extract. These results further suggest that a histamine-like substance or a histamine releaser may be a constituent of nematocyst toxins.

(c) *Action of extracts on the mollusc heart*

The isolated ventricle of the heart of the quahog, *Venus mercenaria*, is a sensitive test object for the bioassay of a variety of quaternary ammonium compounds (WELSH and TAUB, 1948; 1950; 1951). Me_4N and many of its derivatives were known to decrease the amplitude and frequency of heart beat. Some amines, such as adrenaline and tyramine, were known to be excitatory when applied to the isolated *Venus* heart. It was decided to test the action of coelenterate tentacle extracts on an isolated mollusc heart.

Exploratory tests of hearts of several molluscs of the Friday Harbor region indicated that the heart of the horse clam, *Schizothaerus nuttallii*, was highly suitable for determining the action of crude extracts of *Metridium* and *Cyanea* tentacle extracts. Using the isolated ventricle of *Schizothaerus*, as we had previously used the *Venus* ventricle, it was apparent that whole sea-water extracts of tentacles of both *Metridium* and *Cyanea* contained a mixture of heart excitor and inhibitor substances. However, a powerful excitor material usually was dominant and tended to obscure the action of the inhibitor material. The results will not be reported in detail, since later experiments done elsewhere are more readily interpreted. However, a sample set of records, comparing the action of extracts with histamine, deserve to be shown. Fig. 1 shows the marked excitor actions of *Metridium* and *Cyanea* extracts on the *Schizothaerus* heart. The former extract caused an increase in amplitude and frequency and a tonic shortening of the heart (= rise in base line), while the *Cyanea* extract caused an increase in frequency and more marked tonic shortening of the heart. Such differences could be due to relatively greater amounts of the excitor substance in *Cyanea* tentacles.

When histamine was tested on the same heart, it was found to have a weak excitor action when added in an amount to give 0·5 mg histamine dihydrochloride per millilitre of fluid bathing the heart. It is most unlikely that histamine could be the constituent of tentacle extract producing the marked excitation, and we shall see from later experiments that, in fact, it is not. These experiments done at Friday Harbor did, however, prompt further pursuit of the identity of the material with the marked excitor action, and this work will now be reported.

III. OBSERVATIONS MADE AT THE BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY AND THE LABORATORY, PLYMOUTH, ENGLAND

(a) *Evidence for the presence of 5-hydroxytryptamine in tentacle extracts*

In the course of a study of cardio-excitor substances acting on the *Venus* heart, a recently-available indole amine, 5-hydroxytryptamine (5-HT), was tested. It was found to be far more active than other common biological amines such as adrenaline, nor-adrenaline, histamine and tyramine (WELSH, 1953 A). By means of paper chromatography and bioassay, 5-HT was found to occur in the nervous systems of several molluscs, including *Venus mercenaria* (WELSH, 1953 B; 1954). The excitor action of extracts of tentacles of *Metridium dianthus* tested on the *Venus* heart, and of the sea anemone, *Calliactis parasitica*, when tested on the *Buccinum* heart (Fig. 2), so closely paralleled that of 5-HT that an attempt to identify the unknown substance by chromatography was suggested. This was done for extracts of *Metridium* and *Physalia* tentacles, and clear evidence for the occurrence of 5-HT in these extracts was obtained. This study will be reported in some detail elsewhere. When equal weights of body wall and tentacles of *Metridium* were extracted, much more 5-HT was found in tentacles than in body wall. This suggests, but does not prove, that the 5-HT is contained in nematocysts, which are far more numerous on the tentacles than they are in the body wall tissues, even though pieces of acontia were doubtless included with the latter.

5-HT produces pain at a low concentration (10^{-8} g ml) when applied to a blister area on the forearm (ARMSTRONG, DRY, KEELE and MARKHAM, 1953). 5-HT is also a very effective releaser of histamine (FELDBERG and SMITH, 1953). Thus, through direct action or through the release of histamine, 5-HT in nematocyst toxin could be responsible for the itching and burning, as well as the weals and haemorrhagic condition, that may follow contact with certain coelenterates. Recently, JAQUES and SCHACHTER

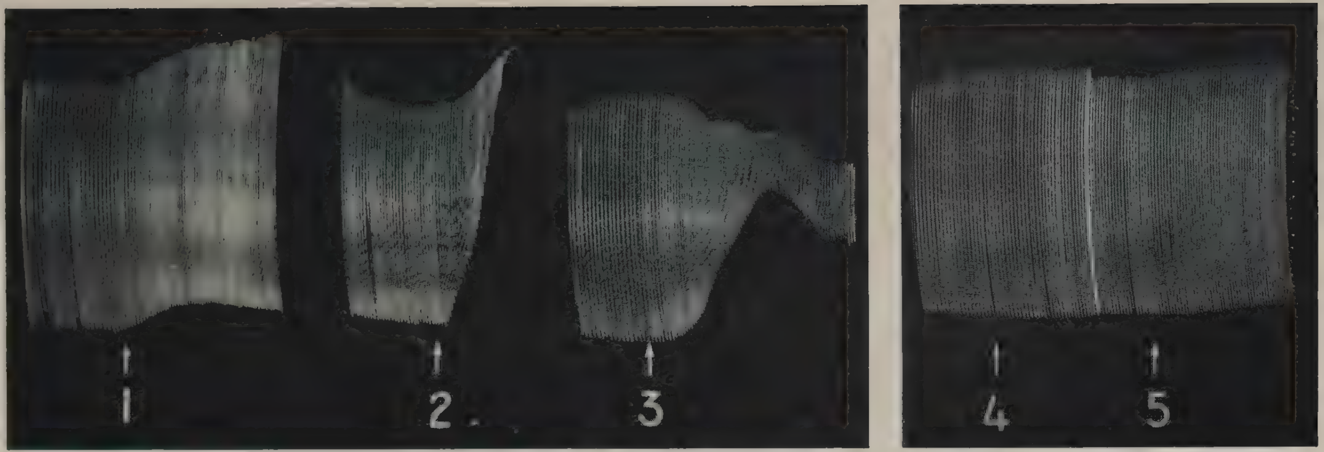

Fig. 1. Action of *Metridium* and *Cyanea* tentacle extracts compared with histamine on the isolated heart of the clam, *Schizothaerus*. Volume of heart bath = 20 ml. Substances added to bath at arrows and action recorded for approximately 3 minutes. A 10 minute period of washing between each test.

(1) 1·0 ml undiluted *Metridium* tentacle extract.
(2) 0·5 ml undiluted *Cyanea* tentacle extract.
(3) 0·1 ml same *Cyanea* extract as in (2).
(4) 1·0 ml 0·1% histamine dihydrochloride.
(5) 1·0 ml 1·0% histamine dihydrochloride.

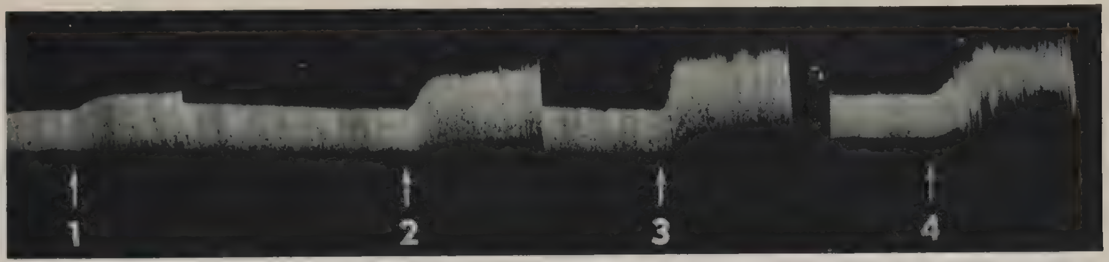

Fig. 2. Effect of extract of *Calliactis parasitica* tentacles compared with 5-hydroxytryptamine on the isolated heart of *Buccinum undatum* (Plymouth, England)

(1) 5×10^{-9} g/ml 5-hydroxytryptamine
(2) 5×10^{-8} g/ml 5-hydroxytryptamine
(3) 5×10^{-7} g/ml 5-hydroxytryptamine
(4) Extract of *Calliactis* tentacles.

(1954 A) have reported the presence of a histamine releaser in alcohol extracts of sea anemone tentacles. These same authors (1954 B) find that histamine and 5-HT are components of the venom of the common European wasp, *Vespa vulgaris*.

At the Plymouth Laboratory in the summer of 1953, 5-HT (in the form of the double sulphate with creatinine)* was injected into a series of *Portunus depurator*. The amounts varied by a factor of ten from 0·0001 mg to 0·1 mg 5-HT per crab. All concentrations produced excitation, as seen in constant movements of walking legs and chelae, with twitching of legs and rapid movements of the pincers. The larger the dose, the more severe were the symptoms. However, this was not followed by paralysis, and within one to two hours the crabs appeared normal. While 5-HT may be responsible for some of the activity of coelenterate toxin, it is clearly not the crustacean-paralyzing factor. When coelenterates are feeding on animals other than crustaceans, it is conceivable that 5-HT could act as a relaxing agent, since it has been found to relax certain molluscan muscle (TWAROG, 1954).

Some of our chromatograms have given a spot which reacts as an indole amine but which has an Rf value differing from that of 5-HT. It is possible that more than one indole amine exists in coelenterates, as is the case in the skin of certain amphibians (ERSPAMER, 1954).

(b) *Chromatographic evidence for the presence of quaternary ammonium bases in tentacle extracts*

Methods outlined by WHITTAKER and WIJESUNDERA (1952) and BREGOFF, ROBERTS and DELWICHE (1953) for the chromatography of quaternary ammonium bases were used in an attempt to determine whether or not tetramethylammonium (Me_4N) (or a derivative) was present in extracts of *Metridium* and *Physalia* tentacles. This led to a more extended study than was originally contemplated. The results to date will be briefly summarized.

Various methods were used to separate quaternary ammonium bases from other materials in acetone extracts of *Metridium* and *Physalia* tentacles. These partially purified bases were placed on paper and chromatographed with a variety of solvents. Ultraviolet absorption and chemical reagents were used to locate the spots. All procedures gave evidence of two or more quaternary ammonium bases present in the extracts in relatively very large amounts. Often only one large spot would be obtained, and added substances, such as Ach or Me_4N, would run with the unknowns rather than separately, thus suggesting a complex of related materials with a carrier substance. When certain areas were eluted and assayed on the *Venus* heart, the eluates inhibited the beat as does Me_4N, Ach or other quaternary ammonium base with two or more methyl groups on the quaternary nitrogen. The action of these eluates was antagonized by Et_4N and Mytolon (cf. WELSH and TAUB, 1953).

We have tentatively identified one of the bases in the extracts as murexine or urocanylcholine. This quaternary ammonium base was found in large amounts in the hypobranchial glands of the Mediterranean snail, *Murex*, by ERSPAMER (1948). It was chemically identified by ERSPAMER and BENATI (1953) after synthesis by PASINI, VERCELLONE and ERSPAMER (1952). A generous sample of synthetic urocanylcholine has recently been received from Dr. PASINI. It should make possible certain identification of the material in the extract, which is clearly a quaternary ammonium base with an ultraviolet absorption spectrum very similar to, if not identical with, that of urocanylcholine.

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* Kindly supplied by Dr. R. K. RICHARDS, Abbott Laboratories.

ERSPAMER and BENATI (1953) report that urocanylcholine (murexine) has intense curariform action. A more detailed account of this phase of their work has not yet been seen. However, it appears that a substance such as murexine might account, at least in part, for the paralyzing action of nematocyst poison. Since the hypobranchial glands of *Murex* also contain large amounts of 5-HT (see ERSPAMER (1954) for references), it could be that a combination of this with urocanylcholine yields a mixture with useful properties in defence and for securing food. It would be strange indeed, should this combination of newly discovered compounds be found in such unrelated structures as the nematocysts of coelenterates and the hypobranchial glands of certain mollusca.

REFERENCES

ACKERMANN, D., HOLTZ, F. and REINWEIN, H. (1923), Reindarstellung und Konstitutionsermittelung des Tetramins, eines Giftes aus *Aktinia equina*. *Zeits. Biol.*, **79,** 113–120.

ALLNUTT, E. B. (1926), Effects of a sting by a poisonous coelenterate. *J. Roy. Army Med. Corps*, **46,** 211–213.

ARMSTRONG, D., DRY, R. M. L., KEELE, C. A. and MARKHAM, J. W. (1953), Observations on chemical excitants of cutaneous pain in man. *J. Physiol.*, **120,** 326–351.

BERNSTEIN, J. (1947), Beware the Portuguese man-of-war. *Nat. Hist.*, **56,** 136–137.

BOISSEAU, J. P. (1952), Recherches sur l'histochimie des cnidaires et de leurs nématocystes. *Bull. Soc. Zool. Fr.*, **77,** 151–169.

BREGOFF, H. M., ROBERTS, E. and DELWICHE, C. C. (1953), Paper chromatography of quaternary ammonium bases and related compounds. *J. Biol. Chem.*, 205, 565–574.

CANTACUZÈNE, J. (1925 A), Action toxique des poisons d'*Adamsia palliata* sur les crustacés décapodes. *C.R. Soc. Biol., Paris*, **92,** 1131–1133.

CANTACUZÈNE, J. (1925 B), Immunité d'*Eupagurus prideauxi*, vis-a-vis des poisons de l'*Adamsia palliata*. *C.R. Soc. Biol., Paris*, **92,** 1133–1136.

CANTACUZÈNE, J. (1926), Activation des poisons de l'*Adamsia palliata* par la lécithine et pouvoir hémolytique. *C.R. Soc. Biol., Paris*, **95,** 118–120.

CANTACUZÈNE, J. and COSMOVICI, N. (1925), Action toxique des poisons d'*Adamsia palliata* sur divers invertébrés marins. *C.R. Soc. Biol., Paris*, **92,** 1464–1466.

CANTACUZÈNE, J. and DAMBOVICEANU, A. (1934 A), Caractères biologiques de l'extrait des acconties d'*Adamsia palliata* après deprotéinisation. *C.R. Soc. Biol., Paris*, **117,** 136–138.

CANTACUZÈNE, J. and DAMBOVICEANU, A. (1934 B), Caractères physicochimiques du poison des acconties d'*Adamsia palliata*. *C.R. Soc. Biol., Paris*, **117,** 138–140.

CANTACUZÈNE, J. and DAMBOVICEANU, A. (1934 C), L'action précipitante spécifique du sérum d'*Eupagurus prideauxi* sur le poison d'*Adamsia palliata*. *C.R. Soc. Biol., Paris*, **117,** 269–271.

COSMOVICI, N. L. (1925 A), L'action des poisons d'*Adamsia palliata* sur les muscles de *Carcinus moenas*. *C.R. Soc. Biol., Paris*, **92,** 1230–1232.

COSMOVICI, N. L. (1925 B), L'action des poisons d'*Adamsia palliata* sur le coeur de *Carcinus moenas*. *C.R. Soc. Biol., Paris*, **92,** 1300–1302.

COSMOVICI, N. L. (1925 C), Les poisons de l'extrait aqueux des tentacules et des nématocystes d'*Adamsia palliata* sont-ils détruits par l'ébullition? Essais d'adsorption. *C.R. Soc. Biol., Paris*, **92,** 1373–1374.

COSMOVICI, N. L. (1925 D), Action convulsivante des poisons d'*Adamsia palliata* sur le *Carcinus moenas* *C.R. Soc. Biol., Paris*, **92,** 1466–1469.

COSMOVICI, N. L. (1925 E), Autotomie chez *Carcinus moenas*, provoquée par les poisons d'*Adamsia palliata*. *C.R. Soc. Biol., Paris*, **92,** 1469–1470.

ERSPAMER, V. (1948), Osservazioni preliminari, chimiche e farmacologiche, sulla murexina. *Experimentia*, **4,** 226–228.

ERSPAMER, V. (1954), Pharmacology of indolealkylamines. *Pharmacol. Revs.*, **6,** 425–487.

ERSPAMER, V. and BENATI, O. (1953), Identification of murexine as β-(imidazolyl-(4))-acryl-choline. *Science*, **117,** 161–162.

FELDBERG, W. and SMITH, A. N. (1953), Release of histamine by tryptamine and 5-hydroxytryptamine. *Brit. J. Pharmacol.*, **8,** 406–*et seq.*

FRACHTMAN, H. J. and MCCOLLUM, W. T. (1945), Portuguese man-of-war stings: a case report. *Amer. J. Trop. Med.*, **25,** 499–500.

JAQUES, R. and SCHACHTER, M. (1954 A), A sea anemone extract (thalassine) which liberates histamine and a slow contracting substance. *Brit. J. Pharmacol.*, **9,** 49–52.

JAQUES, R. and SCHACHTER, M. (1954 B), The presence of histamine, 5-hydroxytryptamine and a potent slow contracting substance in wasp venom. *Brit. J. Pharmacol.*, **9,** 53–58.

McNeil, F. A. (1945), Injuries by unknown agents to bathers in N. Queensland. *Med J. Australia*, **32** (2), 29.

Manunta, C. (1943), La resistenza dei Paguri al veleno della Attinie. Esperienze su *Paguristes oculatus* Fabr. con *Adamsia rondeletii* Andr. *Thalassia, Ist. Italo-Germanico Biol. Mar., Rovigno d'Istria*, **5**, 1–38.

Pasini, C., Vercellone, A. and Erspamer, V. (1952), Synthese des Murexins (β-(Imidazolyl-4(5))-acryl-cholin *Liebig's Ann.*, **578**, 6–10.

Rey, M. (1940), Effets du poison de différentes actinies sur les crustacés décapodes. *Bull. Soc. Zool. France*, **65**, 58–62.

Richet, C. (1902), Du poison pruritogène et urticant contenus dans les tentacules d'Actinies. *C.R. Soc. Biol., Paris*, **54**, 1438.

Richet, C. (1903), Des poisons contenus dans les tentacules des Actinies, congestine et thalassine. *C.R. Soc. Biol., Paris*, **55**, 246.

Richet, C. and Portier, D. (1936), Recherches sur la toxine des coelentérés et les phénomènes d'anaphylaxie. *Rés. Camp. Sci., Monaco*, **95**, 3–24.

Sonderhoff, R. (1936), Über das Gift der Seeanemonen. I. Ein Beitrag zur Kenntnis der Nesselgifte. *Liebig's Ann.*, **525**, 138–150.

Thiel, M. E. (1935), Über die Wirkung des Nesselgiftes der Quallen auf den Menschen. *Ergeb. u. Fortschr. Zool.*, **8**, 1–35.

Twarog, Betty M. (1954), Responses of a molluscan smooth muscle to acetylcholine and 5-hydroxytryptamine. *J. Cell. Comp. Physiol.*, **44**, 141–164.

Wade, H. W. (1928), Post-mortem findings in acute jelly-fish poisoning with sudden death in status lymphaticus. *Amer. J. Trop. Med.*, **8**, 233–241.

Welsh, J. H. (1953 a), Excitation of the heart of *Venus mercenaria*. *Arch. Exp. Path. u. Pharmakol.*, **219**, 23–29.

Welsh, J. H. (1953 b), The occurrence of an excitor amine in the nervous system of *Buccinum* and its action on the heart. *Anat. Rec.*, **117**, 637.

Welsh, J. H. (1954), Hydroxytryptamine: A neurohormone in the invertebrates. *Federation Proc.*, **13**, 162–163.

Welsh, J. H. and Haskin, H. H. (1939), Chemical mediation in crustaceans. III. Acetylcholine and autotomy in *Petrolisthes armatus* (Gibbes). *Biol. Bull.*, **76**, 405–415.

Welsh, J. H. and Taub, R. (1948), The action of choline and related compounds on the heart of *Venus mercenaria*. *Biol. Bull.*, **95**, 346–350.

Welsh, J. H. and Taub, R. (1950), Structure-activity relationships of acetylcholine and quaternary ammonium ions. *J. Pharmacol. and Exp. Therap.*, **99**, 334–342.

Welsh, J. H. and Taub, R. (1951), The significance of the carbonyl group and ether oxygen in the reaction of acetylcholine with receptor substances. *J. Pharmacol. and Exp. Therap.*, **103**, 62–73.

Welsh, J. H. and Taub, R. (1953), The action of acetylcholine antagonists on the heart of *Venus mercenaria*. *Brit. J. Pharmacol.*, **8**, 327–333.

Whittaker, V. P. and Wijesundera, S. (1952), The separation of esters of choline by filter-paper chromatography. *Biochem. J.*, **51**, 348–351.

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Patterns of deposition at the continental margin*

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GENERAL STATEMENT

The term " continental shelf and slope ", " continental terrace ", or " continental platform ", as it has been used for decades in the geological literature, connotes to most geologists the submerged margin of the land masses. But with our rapidly increasing knowledge of submarine geology the fact is becoming apparent that being under water is about the only attribute that many of these areas have in common. It is high time for a reappraisal of what these features really are, and to examine their origin, and to consider critically whether the term should be applied indiscriminately to the submerged margin of any large land mass, no matter how dissimilar the topography and the structure may appear to be.

A continental terrace, as the term will be used here, is a three-dimensional sedimentary structure. The shelf is the shallow, gently sloping upper surface, and the slope is the steep seaward face. It is our purpose here to trace the development of such a sedimentary structure from its earliest beginnings, and to try to show that, where continental margins do not exhibit this simple structure, the answer probably lies in unravelling the varied events of their geologic history rather than in trying to find an oceanographic interpretation. For it is on this point that much of the confusion in the present day literature has arisen as modern marine surveying reveals a bewildering variety of forms. We are fortunate in having preserved two large terraces which have remained basically unaltered ever since their earliest beginnings. For these two terraces, although ancient, are primitive in their structure; they are archetypes, to borrow a term from biology, of many other more complex forms that have evolved in other parts of the globe, whose origin has now been obscured by subsequent events. I refer, of course, to the platforms bordering the eastern and Gulf coasts of the United States. And we are doubly fortunate in that these submerged margins together with their emerged coastal plains have been the sites of intensive geological investigation.

Around the world today the submerged continental margins are of varying widths. The extreme cases are the shelf off Siberia facing the Arctic Basin, three to four hundred miles in width, in contrast to the west coast of South America where the shelf is practically non-existent. At the present time all the continents are largely emergent and the shallow, interior seas which have repeatedly flooded them in the past have largely drained away. Consequently, the continental terraces are now the chief sites where marine sediments are accumulating. There is one major exception to this:

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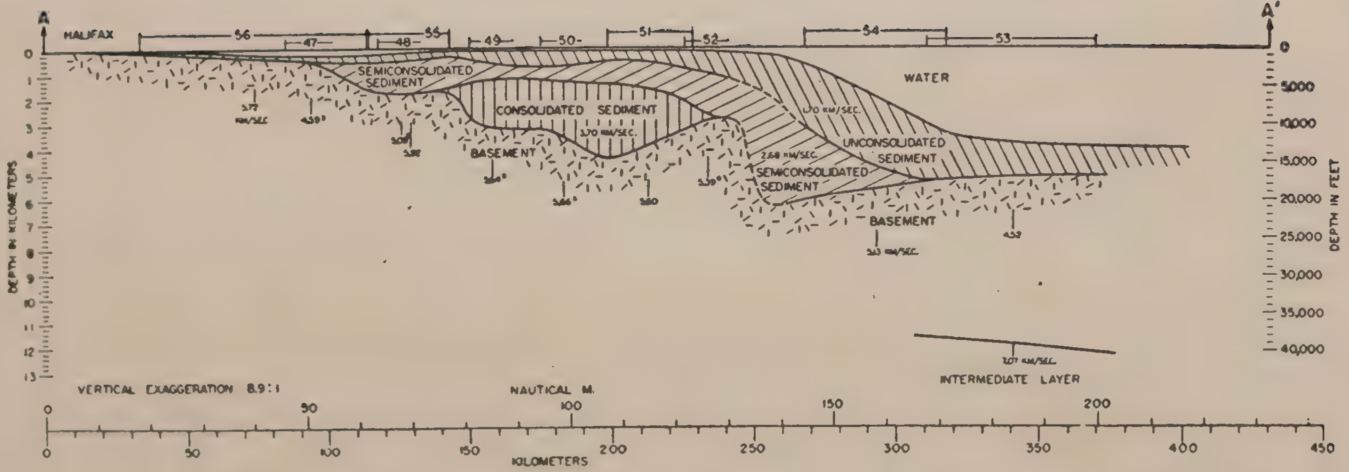
namely the deep basins and shallow inter-island platforms of the East Indies. This, however, is a completely different structural picture, and we will return to this case later.

The investigation of these submerged borderlands, their sediments, topography and structure, is one of the main fields of endeavour in submarine geology today. It should be clearly borne in mind that the present continental slope, however formed, is only a topographic feature and does not represent any sort of boundary between hypothetical continental and oceanic blocks of the crust. In fact, recent seismic work off Nova Scotia and Georges Bank (OFFICER and EWING, 1954) would seem to suggest that there is no difference in the density of the basement complex which underlies this continental terrace, at least to the limits of this particular survey (Fig. 1). The terrace itself is made up of three major divisions of rocks with three distinct velocities. The aprons of detritus which have been deposited on and around continental margins and in marginal geosynclines result in a very complex depositional picture. Progressive orogenies have in many cases further complicated an already intricate stratigraphy. Luckily modern advances in marine geophysics offer some hope that the tangle can some day be unravelled.

THE ATLANTIC AND GULF TERRACES

The Atlantic and Gulf terraces have had a parallel evolution, and, when considering their development, the coastal plain and continental platform should be taken as a unit. In the case of the Atlantic the oldest beds are Lower Cretaceous, and in the Gulf, Jurassic. In simplest terms both are comprised of wedges of inter-fingering continental and marine sediments which thicken in a seaward direction, and in both instances deposition is still going on in the same fashion (Fig. 2). In the Gulf Coastal Plain the formations may be considered a series of truncated wedges lying one on the other, and normal faulting that is contemporaneous with deposition is common (STORM, 1945). This fact should be remembered when the peculiar topography of the Gulf slope is discussed, because the major faults have been traced to the limit of drilling, and furthermore the displacement increases downwards, amounting to hundreds of feet in the older beds, in contrast to but a few near the surface. No such extensive faulting occurs in the Atlantic Plain, although gentle archings and downwarps occur due to basement topography, as is also the case with the Gulf. Both of these terraces have been built unconformably on old erosion surfaces. Updip, where the basement is known, in the western section, the sediments of the Gulf Plain rest on the deformed Palaeozoic rocks of the Ouachita system, and in its eastern portions the Cretaceous laps over the southwestward plunging Appalachians (KING, 1951); downdip the formations have thickened so much that the drill has not reached these rocks or any others which may form the basement in a seaward direction. The surface on which the Atlantic Plain rests is well known throughout due to lesser accumulation. The formations feather out updip against the crystallines of the Fall Line, and a crystalline igneous basement has been reached many times in drilling for oil or water over its whole extent (SPANGLER and PETERSON, 1950; SPANGLER, 1950). It has every appearance of being a peneplaned surface which at present has a gentle seaward dip increasing towards the coastline.

The stratigraphic column at the present shoreline in the Gulf is many times thicker than it is on the Atlantic side; the seas advanced much farther inland and the plains


A
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HALIFAX
56
47
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52
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53
WATER
SEMICONSOLIDATED SEDIMENT
CONSOLIDATED SEDIMENT
3.70 KM/SEC.
BASEMENT
1.70 KM/SEC.
UNCONSOLIDATED SEDIMENT
2.60 KM/SEC.
SEMICONSOLIDATED SEDIMENT
BASEMENT
INTERMEDIATE LAYER
DEPTH IN KILOMETERS
DEPTH IN FEET
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KILOMETERS

Fig. 1. Section across the continental terrace off Halifax, Nova Scotia. (From OFFICER and EWING.)

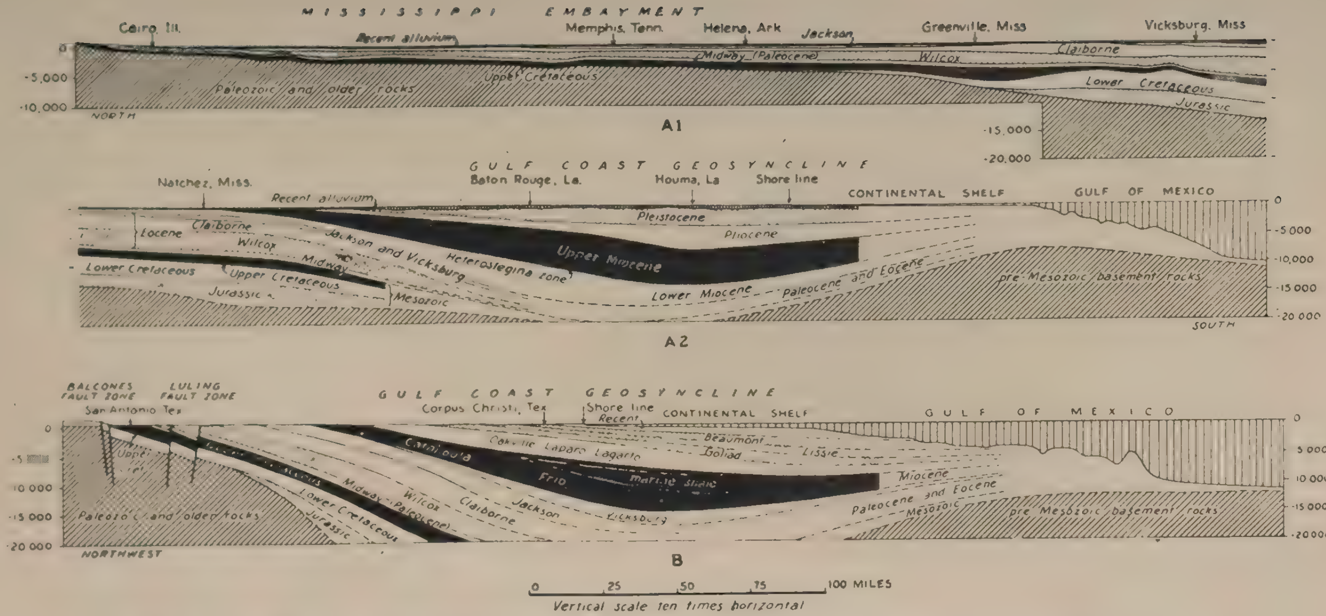
MISSISSIPPI EMBAYMENT
Cairo, Ill.
Memphis, Tenn.
Helena, Ark
Jackson
Greenville, Miss
Vicksburg, Miss
Recent alluvium
Midway (Paleocene)
Wilcox
Claiborne
Upper Cretaceous
Lower Cretaceous
Jurassic
Paleozoic and older rocks
NORTH
0
-5,000
-10,000
-15,000
-20,000
A1
GULF COAST GEOSYNCLINE
Natchez, Miss.
Baton Rouge, La.
Houma, La
Shore line
CONTINENTAL SHELF
GULF OF MEXICO
Recent alluvium
Pleistocene
Pliocene
Eocene
Claiborne
Wilcox
Jackson and Vicksburg
Midway
Heterostegina zone
Upper Miocene
Lower Miocene
Lower Cretaceous
Upper Cretaceous
Jurassic
Mesozoic
Paleocene and Eocene
pre-Mesozoic basement rocks
SOUTH
0
-5,000
-10,000
-15,000
-20,000
A2
BALCONES FAULT ZONE
LULING FAULT ZONE
San Antonio Tex
GULF COAST GEOSYNCLINE
Corpus Christi, Tex
Shore line
Recent
CONTINENTAL SHELF
GULF OF MEXICO
Beaumont
Goliad
Lissie
Catahoula
Frio
Marine shale
Miocene
Paleocene and Eocene
Mesozoic
Upper
Midway-Paleocene
Wilcox
Claiborne
Jackson
Vicksburg
Lower Cretaceous
Jurassic
Paleozoic and older rocks
pre-Mesozoic basement rocks
NORTHWEST
0
-5,000
-10,000
-15,000
-20,000
B
0
25
50
75
100 MILES
Vertical scale ten times horizontal

Fig. 2. (A1 and A2) Generalized section along the axis of Mississippi Embayment from Cairo, Illinois to the continental slope. (B) Generalized section across Gulf Coastal Plain and continental terrace from San Antonio to Corpus Christi, Texas and across the continental terrace. (From King.)

are, therefore, considerably broader. But the same depositional pattern of overlapping lenses is common to each. As Stephenson (1926) observed many years ago in commenting on the stratigraphy of both areas, " The different kinds of materials do not form separate, uniform sheets extending throughout the entire length of the Atlantic and Gulf Plain, for the sediments laid down at any given time differed from place to place and the conditions of sedimentation constantly shifted from time to time. Briefly stated, this means that no two columnar sections, unless closely adjacent to each other, are identical in lithologic succession ". In other words, major and minor transgressions and regressions followed each other with startling rapidity. Deposition has been punctuated by many hiatuses, but the net result has been a growth in thickness and in width, until at present these terraces, coastal plain and continental platforms have attained tremendous proportions, particularly in the Gulf. Since Lower Cretaceous time, then, when both terraces began to assume their present shape, conditions governing transportation and deposition have remained virtually unchanged. The parallel development of these sedimentary wedges affords an excellent illustration of what will happen when a major sea is forced to deal for long periods of time with large supplies of sediment of varying texture over a fluctuating strandline. The same structure will be built along any continental margin; the details will, of course, be modified, depending on the proportions of the variables, but the overall pattern should be recognized. It is not often that the oceanographic and geologic environment has remained so constant for such a long period to permit such a full development.

By way of illustration let us glance briefly at the contemporary oceanographic and sedimentary picture. The Atlantic shelf is, at present, an area of non-deposition, and in places is even undergoing erosion. From New Jersey southwards reworked material from outcropping Coastal Plain formations furnished much of the bottom material, as is evident from the fossils and from the lithology (Stetson, 1936). Consequently, the shelf is predominantly sandy. True, the northern rivers carry little sediment, but although those of the middle and south Atlantic states which do have a large suspended load debouch into bays and sounds, all of the sediment is not trapped in them. What fine material is being delivered to the sea is by-passed to the slope. Cores taken in the silts and clays of varying textures on the slope from Cape Hatteras to New England and in the nearby Atlantic basin show that deposition has been of the order of 50–70 cm since the last cold period, which presumably can be correlated with the last advance of the Wisconsin ice (Stetson, 1949). South of Hatteras the slope and Blake Plateau have generally hard bottoms (*Ibid*, 1949). Temperature and salinity data indicate that the Gulf Stream impinges strongly against this portion of the slope (Iselin, 1936) and sweeps over the surface of the Blake Plateau, preventing any deposition in these two areas.

Turning now to the Gulf shelf, we find what is evidently an area of deposition. Silts of varying textures predominate except for a narrow, sandy strip close to the beach. This is the more usual condition around the world today; it is the large, sandy expanses that are unusual, and the only shelf that is in any way comparable to the one off the eastern United States is found off Argentina. In the case of the Gulf it is probable that more material is being supplied to the sea than it can transport, and the result is that the continental terrace is at present growing at the expense of the Gulf, a process that has been predominant since the beginning of the Tertiary.

The slope is covered with a fine, uniform clay which has a median diameter of about 1 micron, and this texture continues across the bottom of the Sigsbee Deep (STETSON, 1953). This has not always been the case, and, in fact, in the very recent past such uniformity was not present as the cores indicate. For instance, a brown clay now covers the central part of the eastern Gulf, while unconformably below it, at a depth of only a few inches, lies Globigerina ooze.

Our ignorance of bottom currents is profound, and any estimate of bottom velocities must in most cases be based on the grain size of the sediment. It can be taken for granted, for instance, that clean, well sorted sands indicate bottom currents of half a knot or better, conversely, silts and clays can only be deposited under lesser velocities. Waves and tides are the most obvious producers of bottom currents although the competence of the former with increasing depth has recently been questioned (DIETZ and MENARD, 1951). But there can be no question as to the competence of both over the shallower bottoms, and bottom currents from these two sources certainly have higher velocities in the Atlantic than in the Gulf. The winds of Atlantic storms, except for hurricanes, have, by and large, higher velocities and a longer fetch, and are therefore capable of building waves with longer periods. These in turn are capable of moving sedimentary particles at greater depths, and in far greater quantities along the strand, by beach drifting and strong longshore currents. The tidal range on the open Gulf coast is small compared with the Atlantic (roughly 1·5 feet at Galveston, as with 4–5 feet at Delaware Breakwater), and there must be a consequent reduction in the velocities of the tidal currents. I am well aware that this is tantamount to saying that we really don't know how sedimentary particles move over the deeper bottoms; but move they do, as their texture shows. For all intents and purposes, once they are out of sight their transport can only be inferred. There are few quantitative data, and in this direction the oceanographer has so far largely drawn a blank.

PRIMARY TERRACE CONSTRUCTION

Every advance and retreat of the sea leaves its impression on the stratigraphic record, and the numerous unconformities and facies changes exhibited by the overlapping lenses of the Coastal Plain formations are concrete evidence of the numerous oscillations of the strandline. A change of existing sea level, would, in fact, alter the sedimentary distribution which has been described above. For instance, a deepening of the Atlantic shelf would once more make this platform an area of deposition, as it has been many times before.

Under the simplest conditions, during rising sea level, onlap means that the younger deposits overlap the older in a shoreward direction. The nearshore sediments are sandy or gravelly, while the offshore deposits resulting from the same sea-level, and therefore of the same age, will be muddy. In vertical cross-section this eventually results in an overlapping of shales on sandstones. It is a time of continuous accumulation of sediment in a deepening sea, and the continental shelf grows in thickness as well as in width, as successive layers are added to its surface as well as to its forward slope. Conversely, during falling sea-level, offlap means that the younger deposits overlap the older in a seaward direction. As the sea retreats, some of the coarser deposits of the shoal water zone are transported seaward and overlap the older and finer muds which had previously been laid down in deeper water. The surface of the shelf is undergoing erosion, with a reduction in thickness, or perhaps the entire removal of strata deposited near shore during the previous onlap, but it continues to grow in width because deposition is uninterrupted in the deeper water over the seaward slope. Equilibrium, or still stand, will likewise produce a forward growth of the slope; little or nothing is added to the thickness, although there is no loss.

Through all the oscillations of the strand, as well as during periods when sea-level remained constant, the face of the slope always progresses steadily seaward into deeper water. Since Cretaceous time the basement has been sinking with occasional reversals, and the sum total of these oscillatory movements has been downwards. The result has been a terrace constructed of a huge series of overlapping lenses of sediments of diverse lithology. Consequently, although both terraces have grown intermittently in thickness with many depositional breaks, they have grown continuously in width. For example, total thickness of the sedimentary formations along the axis of the geosyncline at the coast near the Texas-Louisiana line has been estimated at more than 40,000 feet (LOWMAN, 1949), but the maximum width of the whole terrace is measured by the 700 odd miles lying between Cairo, Illinois (the high water mark of the Upper Cretaceous seas) and the present continental slope. On the Atlantic side the sedimentary wedge at the shoreline is slightly less than 10,000 feet thick, as logged in an oil well drilled at Cape Hatteras. Offshore, seismic profiles run by the Lamont Geological Observatory indicate a maximum thickness of the order of 16,000 feet in a basin southeast of Delaware Bay, with a rise in the basement seaward near the present continental slope (EWING *et al.*, 1950). Its greatest width is about 175 miles lying on a traverse through Cape May from the Fall Line to the break-in slope. The thickness of the sedimentary prism offshore in the Gulf is, at present, unknown.

TURBIDITY CURRENTS AND SLOPE TOPOGRAPHY

The underwater topography of the Atlantic slope shows a dendritic drainage pattern (VEATCH and SMITH, 1939), characteristic of many land surfaces, of main stream valleys with tributaries, although the streams may have been submarine flows of muddy water known as turbidity currents, and not rivers flowing under the air. Numerous canyons gash the continental slope from Georges Bank to the Chesapeake, and some of them, such as the Hudson, are of considerable size. Perhaps a brief explanation of these submarine streams of muddy water is in order, as they are thought by many geologists to be the erosive agents responsible for the spectacular and enigmatic submarine canyons, which we are now discovering to be world wide. The density of any water mass is increased by a suspended load of sediment. Consequently muddy water will flow under clear water of the same temperature and salinity. Many of the silts and clays of the continental slope have a very high water content, frequently running over 150% of dry weight, and are consequently very unstable and will liquify easily by jarring such as could be produced by a submarine earthquake. Theoretically, the resultant flow may start out as a liquid slump and quickly change into a dense flow of turbid water, thought by some to attain considerable velocity, and hence great erosive power, as it slides down the steep continental slope. Flows of this type have never been observed in the ocean, but gentle turbidity currents are known to flow along the bottom of the whole length of man-made Lake Mead, where the muddy Colorado River plunges beneath the clear waters of that Lake. They have also been observed in some glacial lakes such as Geneva.

What factual data exist at present are all on the depositional side. In areas of low gradients we have the deep sea plains, crossed by the mid-ocean channels with their leveed banks (MENARD, 1955; DIETZ, 1955; HEEZEN *et al.*, 1955), and the same type of channels are found in various Swiss lakes (DALY, 1936). Graded bedding, long a somewhat obscure depositional process, can be best explained by turbidity flows.

So much attention has been focused on the supposed potential energy of the turbidity current by their proponents that the factors that will dissipate this energy such as friction of turbulent flow along boundaries, entraining of clear water, and settling of particles have all but been lost sight of. One source of confusion is the difference between a true turbidity current and a submarine slump or slide. Doubtless a slide starting on a steep slope would eventually grade into a turbidity current, but there must be a great difference in energy at the start as well as in the mechanics of their motion and their erosive power. Witness the conflict of opinion over the velocities and even the type of the Grand Banks " flow " which parted the Western Union cables following the earthquake of 1928 (KULLENBERG, 1954). Possibly this may seem academic, but when the term " turbidity current " is mentioned many people visualize a suspension current such as flows along the bottom of Lake Mead or in the Swiss lakes. These patently have no erosive power; and it is not a question of having a super Colorado River and producing a turbid suspension of greater volume. Possibly a mud or sediment slide or flow would be a better term to apply to the initial slump of unstable sediment failing under gravitational stress, restricting turbidity current to the transporting and depositing agent. When looked at objectively, the dynamic role assigned to density currents by their advocates may be seen to have more than a tinge of wishful thinking induced by an attempt to escape from the horns of a dilemma. Obviously an enormous amount of vigorous erosion must have taken place to cut the submarine canyons and to make matters worse, during the late glacial period, which is only yesterday. Conventional rivers would require more relative displacement of land and sea than most geologists will admit is probable or possible. To circumvent this, the turbidity current has been hailed almost overnight as the answer to all vexing problems of submarine erosion,

The topography of the continental slope in the northwestern Gulf of Mexico is very complicated as GEALY (1955) has pointed out, and, according to her analysis, has probably been produced by a variety of causes. Sub-aerial erosion, the failure of unstable sediments which are under shearing stress, salt domes and crustal faulting have all played a part. An extensive scarp bounds the Sigsee Deep and continues around the continental slope off the west Florida platform, where it is found to be over 7000 feet high (JORDAN, 1951 and Fig. 3). Pronounced normal faulting could be the only cause for cliffs such as these. Higher up on the slope the troughs and ridges and hummocky topography is thought to be the surface expression of lesser shearing at depth plus erosion by sediment flows and slumps. The material is largely furnished by the thick Pleistocene deposits lying on the upper parts of the slope.

MOBILE CONTINENTAL MARGINS

As an historical background to the existing terraces, consider the " long succession of geosynclines of differing kinds and trends " with their attendant island arcs, such as has been postulated by many authors (KAY, 1951) lying along the Atlantic and Gulf margins during Palaeozoic time. In a situation such as this the supply of detritus comes from within the orthogeosynclines themselves, from fluctuating upwarps of their floors, from volcanoes and igneous intrusions, and from the islands themselves. The volcanic rocks within the sedimentary series seem to be restricted to what are termed the eugeosynclines, while the miogeosynclines contain only sediments. This is in direct contrast to the views of those who consider the hypothetical continent of Appalachia lying somewhere near the present 100 fathom line the sole source. The Dutch East Indies have been cited as a modern large-scale parallel to the paleogeography along the eastern seaboard and along the Gulf during the Palaeozoic.

Temporarily at least, orogenic activity and vulcanism has ceased along the eastern and Gulf coasts of the United States; and the parallel geosynclinal belts, the Appalachian, the Ouachita and the Witchita systems, have long been quiescent. The net result since Cretaceous time has been the construction of two " paraliageosynclines " according to KAY's terminology. These are linear troughs of undeformed sediments lying along the outer margins of the geosynclinal belts, and their seaward limits form the present continental slope. Obviously their strata, which in the case of the Atlantic and Gulf are thickening seaward at the present shoreline, must thin as the outer margins are reached, but there are few data on this point.

Continental terraces like these obviously need an extensive hinterland to supply the sediments if they are to reach any sizable proportions, and furthermore the drainage must be into the ocean. These conditions are not always met, which may be the explanation for our inability to find comparable structures built during the Palaeozoic. KUENEN (1950) has speculated on what could have happened to them, reasoning that, because of the much greater interval of time that was available for their building, such structures would not be easy to hide. It well may be, however, that under mobile geosynclinal conditions they never existed.

Specifically, in the case which we are considering here, the two terraces are now building on what are probably the bevelled surfaces of the rocks forming the outer parts of the Palaeozoic eugeosynclines peneplaned after orogenic and plutonic activity had ceased. They serve as models of the simple forms which will be constructed by the processes of marine transportation and deposition when these operations are not interfered with by activity in the mobile belts.

The sediments, topography and structure of but very few submerged continental areas are well enough known to warrant critical comment. Aside from the two under discussion, we have only the areas off California, Norway, the West Indies, and Indonesia, for which adequate bathymetric charts exist. Some oceanic areas have been charted in considerable detail, but they have no bearing on this problem. The East Indies have already been mentioned as a modern illustration of deposition in eugeosynclines and miogeosynclines. The West Indies present a somewhat analogous case, but very little is known about the sediments.

Off California the sedimentary platforms have been extensively faulted and tectonically broken up into numerous basins and ridges. Occasional granitic outcrops have been found in the walls of a few of the minor, nearshore submarine canyons, but extensive rock dredging shows that they are only small intrusions and that the continental terrace, like that in the Atlantic, is composed of Cretaceous and Tertiary sediments. Nothing is known about the basement. The continental slope along the entire margin is in many cases controlled by long fault scarps of considerable displacement (SHEPARD and EMERY, 1941). The same is true of the walls of the deep

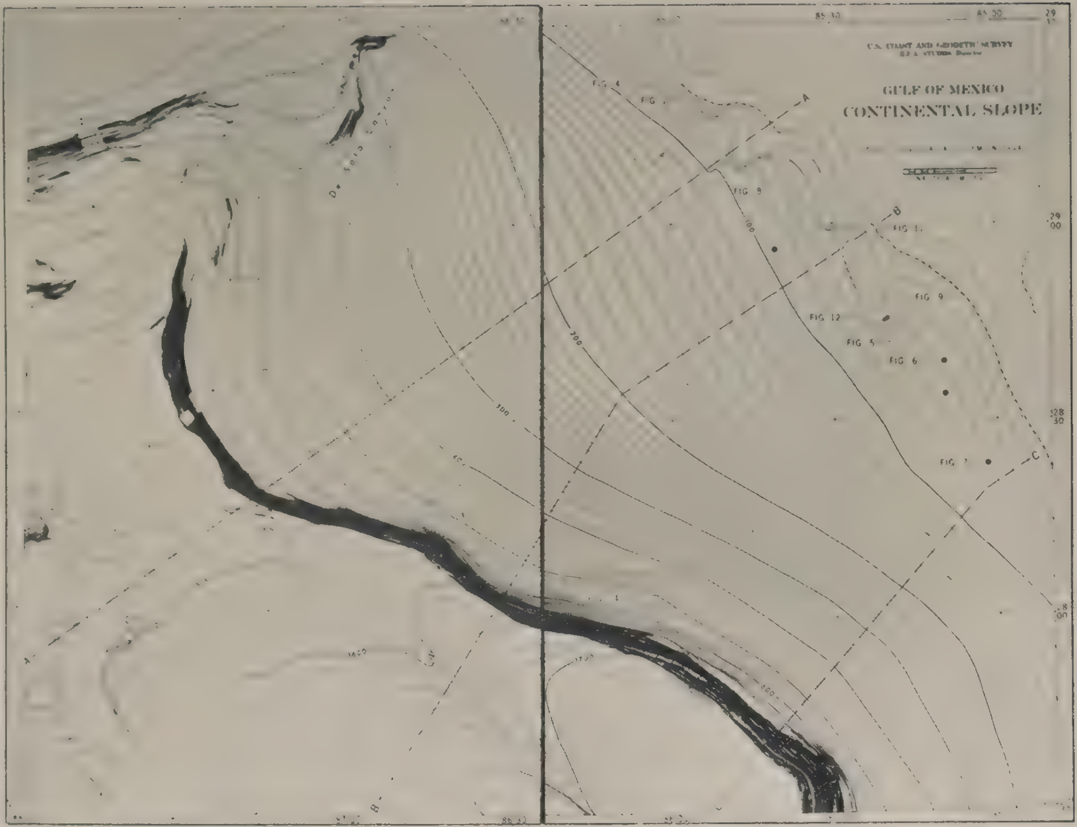
U.S. COAST AND GEODETIC SURVEY
GULF OF MEXICO
CONTINENTAL SLOPE
A
B
C
FIG 4
FIG 9
FIG 1
FIG 12
FIG 5
FIG 6
FIG 7
100
200
De Soto Canyon
29 00
28 30
28 00
85 30
85 00

Fig. 3. A portion of the fault scarp forming the continental slope off the west Florida platform. (From JORDAN).

basins which are so characteristic of the southern section. The continental slope off the west Florida platform (Fig. 3) represents the most striking submarine fault scarp known at present, in places attaining a height of over 7000 feet. This can be traced around the Keys into Florida Strait, but its height has diminished to about 600 feet (Jordan, 1954).

Holtedahl (1950) concluded that the Norwegian shelf consists of consolidated rock which probably belongs to the same complex which makes up the hinterland, that is, granites and metamorphics, and that the whole is partially covered with a veneer of glacial debris of all types. The slope is controlled by what are apparently a series of step faults. Obviously, any comparisons as regards a depositional origin of the slope can no longer be made in this case, and there is nothing now to suggest a sedimentary origin for this entire borderland. Possibly it represents the eroded roots of a former eugeosyncline upon which no " paraliageosyncline " has been built, for lack of an adequate area from which the sediments might have been supplied.

A case that appears to be somewhat analogous is found off the end of the Breton Peninsula. Extensive areas of rocky bottom extending out towards the continental slope are shown on the chart of bottom lithology appearing in the Atlas de France for 1935, with Dangeard as the authority. It would be reasonable to suppose that the igneous complex making up this peninsula plunges beneath the sea, although there is no notation of rock types, and there are no charts which give any clear picture of bottom topography.

There is enough diversity in the examples cited above to make the geologist pause before assigning any blanket mode of formation to the continental shelf and slope. It is not our purpose here to review the older mechanical theories such as the abrasion platform and the marine delta. Today they have few adherents (Dietz, 1952). It is becoming apparent that each continental margin must be studied on its own merits; its history, structure and lithology must be known, and we must also know something about the oceanographic conditions which control sedimentation beyond the coastline. Without adequate marine topographic surveys we are still only guessing, and these must be supplemented by bottom coring and dredging. The case presented here for offlap and onlap is an attempt to reduce the sedimentary picture to its simplest, most primitive terms, in situations where oceanographic conditions have remained constant for long periods of time. From this point on it will be obvious to anyone that an endless succession of variables can be introduced to alter the pattern of the prototype.

REFERENCES

Daly, R. A. (1936), Origin of submarine " canyons ". *Amer. J. Sci.*, **31** (186), 401–420.

Dietz, R. S. (1952), Geomorphic evolution of continental terrace (continental shelf and slope). *Bull. Amer. Assoc. Petrol. Geol.*, **36** (9), 1802–1819.

Dietz, R. S. (1954), Possible deep sea turbidity current channels in the Bay of Bengal. *Current Sci.*, **23** 254–256.

Dietz, R. S. and Menard, H. W. (1951), Origin of abrupt change in slope at continental shelf margin. *Bull. Assoc. Petrol. Geol.*, **35** (9), 1994–2016.

Ewing, M., Worzel, J. L., Steenland, N. C. and Press, F. (1950), Geophysical investigations in the emerged and submerged Atlantic Coastal Plain. Part V: Woods Hole, New York and Cape May sections. *Bull. Geol. Soc., Amer.*, **61** (9), 877–892.

Gealy, B. L. (1955), Topography of the continental slope in Northwest Gulf of Mexico. *Bull. Geol. Soc., Amer.*, **66** (2), 203–227.

Heezen, B. C., Ewing, M. and Ericson, D. B. (1955), Reconnaissance survey of the abyssal plain south of Newfoundland. *Deep-Sea Res.*, **2** (2), 122–133.

HOLTEDAHL, H. (1951), A study of the topography and sediments of the continental slope west of Møre, W. Norway. *Univ. i Bergen. Arbok* 1950, Naturvidensk. rekke, (5), 1–58.
ISELIN, C. O'D. (1936), A study of the circulation of the Western North Atlantic. *Pap. Phys. Oceanogr. Meteorol.*, **4** (4), 1–101.
JORDAN, G. F. (1951), Continental slope off Apalachicola River, Florida. *Bull. Amer. Assoc. Petrol. Geol.*, **35** (9), 1978–1993.
JORDAN, G. F. (1954), Large sink holes in the Straits of Florida. *Bull. Amer. Assoc. Petrol. Geol.*, **38** (8), 1810-1817.
KAY, M. (1951), North American geosynclines. *Geol. Soc. Amer. Mem.*, **48** 1–143.
KING, P. B. (1951), The tectonics of Middle North America. Princeton Univ. Press, Princeton, N.J., 224 pp.
KUENEN, PH. H. (1950), The formation of the continental terrace. *Adv. Sci.*, 7 (5), 76–80.
KULLENBERG, B. (1954), Remarks on the Grand Banks turbidity current. *Deep-Sea Res.* **1** (4), 203–210.
LOWMAN, S. W. (1949), Sedimentary facies in Gulf Coast. *Bull. Amer. Assoc. Petrol. Geol.*, **33** (12), 1939–1997.
MENARD, H. W. (1955), Deep-sea channels, topography and sedimentation. *Bull. Amer. Assoc. Petrol Geol.*, **39** (2), 236-255.
OFFICER, C. B. and EWING, M. (1954), Geophysical investigations in the emerged and submerged Atlantic Coastal Plain. Part VII: Continental shelf, continental slope, and continental rise south of Nova Scotia. *Bull. Geol. Soc., Amer.*, **65** 653–670.
SHEPARD, F. P. and EMERY, K. O. (1941), Submarine topography off the California coast: Canyons and tectonic interpretation. *Geol. Soc., Amer., Spec. Pap.* No. 31, 1–171.
SPANGLER, W. B. (1950), Subsurface geology of Atlantic Coastal Plain of North Carolina. *Bull. Amer. Assoc. Petrol. Geol.*, **34** (1), 100–132.
SPANGLER, W. B. and PETERSON, J. J. (1950), Geology of the Atlantic Coastal Plain in New Jersey, Delaware, Maryland, and Virginia. *Bull. Amer. Assoc. Petrol Geol.*, **34** (1), 1–99.
STEPHENSON, L. W. (1926), Major features in the geology of the Atlantic and Gulf Coastal Plain. *J. Washington Acad. Sci.*, **16** (17), 460–480.
STETSON, H. C. (1936), Geology and paleontology of the Georges Bank canyons. Part 1, Geology. *Bull. Geol. Soc. Amer.*, **47** (3), 339–366.
STETSON, H. C. (1949), The sediments and stratigraphy of the east coast continental margin, Georges Bank to Norfolk Canyon. *Pap. Phys. Oceanogr. Meteorol.*, **11** (2), 1–60.
STETSON, H. C. (1953), The sediments of the Western Gulf of Mexico. Part 1. The continental terrace of the Western Gulf of Mexico: its surface sediments, origin and development. *Pap. Phys. Oceanogr. Meteorol.*, **12** (4), 1–45.
STORM, L. W. (1945), Resume of facts and opinions on sedimentation in Gulf coast region of Texas and Louisiana. *Bull. Amer. Assoc. Petrol Geol.*, **29** (9), 1304–1335.
VEATCH, A. C. and SMITH, P. A. (1939), Atlantic submarine valleys of the United States and the Congo submarine valley. *Geol. Soc., Amer., Spec. Pap.* No. 7, 1–101.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 309-320.

Scaphopods of the *Atlantis* dredgings in the Western Atlantic with a catalogue of the scaphopod types in the Museum of Comparative Zoölogy *

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The following report is based mainly on the collection of scaphopods made by the *Atlantis* in 1938 and 1939 during two trips to Cuba. A small amount of hitherto unworked material in the collection of the Museum of Comparative Zoölogy is also recorded where it is of significance in the distribution of the species concerned. This material includes a number of lots collected by the late Dr. Leo A. Burry of Pompano Beach, Florida, who did a great deal of dredging off the Florida Keys and in the region off Fort Walton, Florida. In addition there are several lots of *Blake* and *Hassler* material that had not been previously worked, as well as miscellaneous lots that have come in from various sources. Localities given by Henderson (1920) have not been duplicated in this report; all records are of new localities or new depth records.

Though there are no new species in this material, it is of great value in extending the ranges of many species, and in several cases these constitute the second known record for the species. Except for a few intertidal species which may be common, records of scaphopods are always rare, consequently it seems advisable to put these new data on record. This is especially important since Henderson's report is relatively recent and quite complete, so that a new monograph probably will not be attempted for some time.

It is interesting to compare the results of the *Atlantis* trips with those of the Johnson-Smithsonian Expedition to the Puerto Rican Deep as reported by W. K. Emerson (1952). Both collected fifteen species which could be positively identified, and of these only eight were taken by both, which would indicate a purely chance factor in collecting. Undoubtedly many species are far more widely and evenly distributed than would appear from the published record. Only after continued dredging over a long period of time will it be possible to derive accurate distribution patterns of these deep-sea groups. When sufficient material is collected, most of the subspecies and even some of the species now recognized will probably be shown to be mere populations of widespread, polymorphic species. This was certainly evident from the study of the material covered in this present report. In most cases classification has been to species only, as it would appear that many of Henderson's subspecies are of doubtful value; in many cases the ranges of two subspecies overlap almost completely.

According to his introduction, Henderson, at the time he wrote his monograph, had the entire collection of the Museum of Comparative Zoölogy for study; however,

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* Contribution No. 779 of the Woods Hole Oceanographic Institution.

except in rare cases and in the case of a few types, he made no mention of this material. Much of the *Blake* material is in the Museum of Comparative Zoölogy and in most cases the specimens figured and so labelled by DALL, are contained in this collection. A catalogue of all of the types of Western Atlantic scaphopods in the Museum collection is appended to this report for the convenience of interested workers.

HENDERSON gave an excellent historical account of the work done in this group up to 1920, consequently only a brief bibliography is given here. No attempt has been made to describe the various species, for descriptions and figures may be found in the works of WATSON (1895); DALL (1889); PILSBRY and SHARP (1898) and HENDERSON (1920). The classification to genera and subgenera follows that of HENDERSON.

Maps indicating the course of the *Atlantis* during the two circumnavigations of Cuba in 1938 and 1939, together with a complete list of the stations, are given by CHACE (1940). Unfortunately, several localities where the *Blake* and the *Atlantis* did a small amount of dredging were not given station numbers. Consequently in this report where reference is made to the ship without station number it is because none was allotted.

NEW SCAPHOPOD RECORDS FOR THE WESTERN ATLANTIC

Dentalium (Dentalium) laqueatum Verrill

Dentalium laqueatum VERRILL 1885, Trans. Connecticut Acad. Arts and Sci. **6**, pt. 2, p. 431, pl. 44, fig. 18; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 23, pl. 1, figs. 6–7.

Notes. Though HENDERSON lists a large number of lots for this species, they are largely restricted to the region of Cape Hatteras, North Carolina and to the Lower Florida Keys. The following *Atlantis* records extend our knowledge of its distribution to Cuba. One exceedingly large specimen from off Punta Alegre, Cuba, measured 85 mm in length, or 23 mm longer than any previously recorded. HENDERSON's subspecies *regulare* appears to be of doubtful value. Its range overlaps that of the typical form and, in addition, in the typical form there appears to be a wide range of variation in the strength of the secondary costae.

Records. CUBA: *Atlantis*, station 2963, off Bahía de Cochinos, Las Villas (N. Lat. 22′ 07′. W. Long. 81° 08′) in 180–190 fathoms; *Atlantis*, station 2982E, off Punta Alegre, Camagüey (N; Lat. 22° 45′; W. Long. 78° 45′) in 150–180 fathoms; *Atlantis*, station 2999, off Bahia de Matanzas, Matanzas (N. Lat. 23° 10′; W. Long. 81° 29′) in 145–230 fathoms.

FLORIDA: off Carysfort Light, Key Largo in 66–117 fathoms (L. A. BURRY—5 lots); off Beacon D, Key Largo in 65–108 fathoms (L. A. BURRY—2 lots); 3½ miles N.E. of Pacific Reef, Key Largo in 66 fathoms (L. A. BURRY).

Dentalium (Dentalium) obscurum Dall

Dentalium gouldii obscurum DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 425, pl. 27, fig. 4.
Dentalium obscurum DALL, HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 32, pl. 3, figs. 1, 3.

Notes. This is an exceedingly rare though probably widely distributed species. DALL thought it was only a variety of *gouldii* but I agree with HENDERSON that it is quite a different species. It has previously been known only from the Barbados, where it has been collected several times.

Records. CUBA: *Blake*, station 62, off Habana in 80 fathoms.

Dentalium (Dentalium) carduum Dall

Dentalium carduus Dall 1889, Bull. Mus. Comp. Zoöl. **18**, p. 423, pl. 27, fig. 3; Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 33, pl. 3, figs. 4, 5, 7.

Notes. Five lots of this rare species were taken by the *Atlantis*, and these are the first recorded for Cuba and Florida. The species is probably widespread throughout the West Indies for, though only eleven lots are known, they are distributed from the Little Bahama Bank, south to Cuba, St. Thomas, Grenada and Barbados. One large specimen taken by the *Atlantis* measured 10 mm in greatest diameter, and if complete would probably have measured some 95 mm in length, or some 8 mm greater than the largest recorded specimen.

Records. FLORIDA: *Atlantis*, station 2951, about 55 miles off Fort Lauderdale (N. Lat. 26° 08′; W. Long. 79° 02′) in 155 fathoms. CUBA: *Atlantis*, station 2982A (N. Lat. 22° 48′; W. Long. 78° 50′) in 210 fathoms; *Atlantis*, station 2981D (N. Lat. 22° 48′; W. Long. 78° 51′) in 190–230 fathoms; *Atlantis*, station 2982E (N. Lat. 22° 45′; W. Long. 78° 45′) in 150–180 fathoms; *Atlantis*, station 2980A (N. Lat. 22° 48′; W. Long. 78° 41′) in 220–260 fathoms. All the above are from off Punta Alegre, Camagüey, Cuba.

Dentalium (Antalis) entale stimpsoni Henderson

Dentalium striolatum Stimpson 1851, Proc. Boston Soc. Nat. Hist. **4**, p. 114 (non *D. striolatum* Risso 1826).

Dentalium entale stimpsoni Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 35 (new name for *striolatum* Stimpson, non Risso 1826).

Notes. Only one lot of this rather common northern species was obtained by the *Atlantis*. Though there are many lots in the collection of the Museum of Comparative Zoölogy they do not extend the range beyond that given by Henderson.

Records. *Atlantis*, station 2661, off Nova Scotia (N. Lat. 43° 40′; W. Long. 67° 49′) in 126 fathoms.

Dentalium (Antalis) antillarum d'Orbigny

Dentalium antillarum d'Orbigny (in) Sagra, Histoire l'Ile de Cuba, *Mollusques*, Atlas pl. 25, figs. 10–13; ibid. 1847, text **2**, p. 202; Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 44, pl. 5, figs. 1–4, 6–8

Notes. Though this more shallow water species was not collected by the *Atlantis*, several lots in the Museum collection are from localities not previously reported and so seem worthy of note here. These were collected largely by William J. Clench.

Records. BAHAMA ISLANDS: Simms, Long Island; Arthurs Town, Cat Island; Little San Salvadore, 18 miles W. of Cat Island. HISPANIOLA: Cape Haitien, Haiti; Monte Cristi, Santo Domingo. PUERTO RICO: Lóiza Vieja. LESSER ANTILLES: Guadeloupe.

Dentalium (Antalis) disparile d'Orbigny

Dentalium disparile d'Orbigny 1842, (in) Sagra, Histoire l'Ile de Cuba, *Mollusques*, Atlas pl. 25, figs. 14–17; ibid. 1847, text **2**, p. 202; Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 47, pl. 6, figs. 4–8.

Notes. Henderson records only eleven lots for this species and, though it was not taken by the *Atlantis*, two new records are noted.

Records. TRINIDAD: Gaspari. BRASIL: Maranhão.

Dentalium (Antalis) ceratum Dall

Dentalium ceratum Dall 1881, Bull. Mus. Comp. Zoöl. **9**, p. 38; Dall 1889, Bull. Mus. Comp. Zoöl. **18**, p. 424, pl. 26, fig. 5, pl. 27, fig. 2; Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 49, pl. 7, figs. 2–7.

Notes. The lot collected by the *Atlantis* at station 2996 greatly extends the depth at which this species is known to live. Henderson's subspecies *flavum* and *tenax* appear to be the only variants with no geographic significance, for it has been possible to find gradients between these and the typical form.

Records. FLORIDA: 3½ miles N.E. of Pacific Reef, Key Largo in 66 fathoms (L. A. Burry). CUBA: *Atlantis*, station 2996, off Bahía de Cardenas, Matanzas (N. Lat. 23° 22′; W. Long. 81° 05′) in 470–665 fathoms; *Atlantis*, station 2963, off Bahía de Cochinos, Las Villas (N. Lat. 22° 07′; W. Long. 81° 08′) in 180–190 fathoms.

Dentalium (Antalis) taphrium Dall

Dentalium taphrium Dall 1889, Bull. Mus. Comp. Zoöl. **18**, p. 422; Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 53, pl. 7, fig. 8.

Notes. This is a very characteristic species. It generally lives in depths from about 20 to 120 fathoms. The specimen from Yucatan Straits in 640 fathoms was dead at the time it was collected, and it does not necessarily follow that the species lives at such depths.

Records. MEXICO: *Blake* station, Yucatan Straits in 640 fathoms. FLORIDA: off Beacon D, Key Largo in 38–100 fathoms (6 lots); off Carysfort Light, Key Largo in 100–117 fathoms (2 lots); off Molasses Reef, Ley Largo in 66–75 fathoms (2 lots); 3 miles S.E. of Sombrero Light, Marathon in 58 fathoms (all L. A. Burry).

Dentalium (Antalis) bartletti Henderson

Dentalium (*Antalis*) *bartletti* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 55, pl. 8, figs. 2, 7.

Notes. Specimens taken by the *Atlantis* off Puerto Sagua la Grande and Puerto de Tánamo were 66 mm and 74·5 mm long respectively, the latter being 19·5 mm longer than Henderson's largest specimen.

Records. CUBA: *Atlantis*, station 2991, (N. Lat. 23° 21′; W. Long. 80° 23′) in 475 fathoms; *Atlantis*, station 2988, (N. Lat. 23° 15′; W. Long. 79° 57′) in 380 fathoms; *Atlantis*, station 2989 (N. Lat. 23° 10′; W. Long. 80° 04′) in 360 fathoms,—All off Puerto Sagua la Grande, Las Villas; *Atlantis*, station 3370, off Puerto de Tánamo, Oriente, (N. Lat. 20° 47′; W. Long. 75° 11′) in 450 fathoms; *Blake*, station, off Bahía Honda, Pinar del Río in 418 fathoms. BRITISH HONDURAS: *Blake*, station 18, off Belize (N. Lat. 18° 08′; W. Long. 87° 16′) in 600 fathoms. LESSER ANTILLES: *Blake*, station 265, off Grenada (N. Lat. 12° 03′; W. Long. 61° 49′) in 576 fathoms.

Dentalium (Fissidentalium) meridionale verrilli Henderson

Dentalium solidum Verrill 1884, Trans. Connecticut Acad. Arts and Sci. 6, p. 215, pl. 44, fig. 16 (non *D. solidum* Hutton 1873).

Dentalium (*Fissidentalium*) *meridionale verrilli* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 62, pl. 9, fig. 3,

Notes. A number of lots of this rather common northern species were collected by the *Atlantis* while working along the continental slope from New Jersey to Virginia. This is a large, strong species and one of the few that are readily obtained in large numbers by a dredge, and, at the same time, are not broken in the process. This fact probably accounts for its greater abundance in collections, and therefore the belief that it is common, though perhaps it is no more so than many other species.

Records. NEW JERSEY: *Atlantis*, 4 stations, off Cape May in 935–1050 fathoms; *Atlantis*, 2 stations, off Little Egg Harbor in 820 and 935 fathoms; *Atlantis*, 2 stations, off Point Pleasant in 1105 and 1230 fathoms; *Atlantis*, off Long Branch in 520 fathoms. DELAWARE: *Atlantis*, station (N. Lat. 38° 31′; W. Long. 73° 03′) in 915–975 fathoms. MARYLAND: *Atlantis* station, off Assateague Bay (N. Lat. 39° 05′; W. Long. 73° 30′) in 970 fathoms. VIRGINIA: *Atlantis* station, off Accoma (N. Lat. 37° 43′; W. Long. 73° 40′) in 1105 fathoms.

Dentalium (Graptacme) eboreum Conrad

Dentalium eboreum CONRAD 1846, Proc. Acad. Nat. Sci. Philadelphia **3**, p.37; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 66, pl. 10, figs. 3–5, 8–9; pl. 11, fig. 6.

Notes. This may be a very common species in some localities. It lives apparently in fairly shallow water and down to depths of 80 to 100 fathoms. The shells being solid and strong are often washed up on the beaches in considerable numbers. The following data add to the distribution records of this species on the west coast of Florida and extend the range to Mustang Island, Texas.

Records. FLORIDA: Clearwater; Gulfport; Bradenton Beach. TEXAS: Mustang Island.

Dentalium (Graptacme) semistriolatum Guilding

Dentalium semistriolatum GUILDING 1834, Trans. Linn. Soc. London **17**, pt. 1, p. 34, pl. 3, figs. 1–6; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 69, pl. 11, figs. 1–3, 8–9.

Notes. Several additional records of this rather common West Indian species are added. The one from off Fort Walton, Florida, adds one more species to the list of West Indian forms that are found in deeper water in the northern Gulf. The record for Swan Island carries the distribution of the species well into the western Caribbean.

Records. FLORIDA: 15–35 miles off Fort Walton in 13–19 fathoms (L. A. BURRY). CUBA: Pueblo Nuevo and Cárdenas, Matanzas Bay, Matanzas. VIRGIN ISLANDS: Virgin Gorda. HISPANIOLA: Monte Cristi, Santo Domingo; LESSER ANTILLES: Guadeloupe. [CARIBBEAN ISLANDS: Swan Island in 60 fathoms.

Dentalium (Graptacme) calamus Dall

Dentalium calamus DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 421; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 72, pl. 12, figs. 7–8.

Notes. This is a rare but very characteristic species which is found in rather shallow water. The two records from the Bahamas were collected by Owen Bryant.

Records. BAHAMA ISLANDS: Whale Cay Channel, Great Abaco Island in 3 fathoms; Dick's Point, Nassau, New Providence.

Dentalium (Laevidentalium) callipeplum Dall

Dentalium callipeplum DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 419, pl. 27, fig. 12b; HENDERSON 1920, Bull U.S. Nat. Mus. No. 111, p. 74, pl. 12, fig. 5.

Notes. A very large, fine specimen of this rare species was collected by the *Atlantis* in 2075 fathoms, which greatly extends the known depth for this species.

Records. FLORIDA: 2½ miles E.S.E. of Beacon D, Key Largo in 58 fathoms (L. A. BURRY). CUBA: *Atlantis*, station 2964, Banco Paz, Las Villas (N. Lat. 20° 56′; W. Long. 80° 11′) in 2075 fathoms. VIRGIN ISLANDS: St. Thomas (T. BLAND).

Dentalium (Laevidentalium) perlongum Dall

Dentalium perlongum DALL 1881, Bull. Mus. Comp. Zoöl. **9**, p. 36; DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 419, pl. 27. fig. 6; HENDERSON, 1920, Bull. U.S. Nat. Mus. No. 111, p. 75, pl. 9, fig. 1.

Notes. Four fine lots, one of them with 8 specimens, were collected by the *Atlantis*. The following are apparently the first Cuban records for this species.

Records. *Atlantis*, station 2992B, off Bahía de Santa Clara, Matanzas (N. Lat. 23° 26′; W. Long. 80° 28′) in 535 fathoms; *Atlantis*, station 2993, off Bahía de Santa Clara (N. Lat. 23° 24′; W. Long. 80° 44′) in 580 fathoms; *Atlantis*, station 3345, off Banco Paz, Las Villas (N. Lat. 21 08′; W. Long. 79° 56′ 30″) in 700 fathoms; *Atlantis*, station 3370, off Puerto de Tánamo, Oriente (N. Lat. 20° 47′; W. Long. 57° 11′) in 450 fathoms.

Dentalium (Episiphon) sowerbyi Guilding

Dentalium sowerbyi GUILDING 1834, Trans. Linn. Soc. London **17,** p. 35, pl. 3, fig. 7; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 77, pl. 13, figs. 2–3, 10.

Notes. L. A. BURRY obtained this species at seven stations during his dredging off Key Largo. It is a very small but characteristic and easily recognized species.

Records. FLORIDA: off Beacon D, Key Largo in 66–90 fathoms (4 lots); off Carysfort Light, Key Largo in 92 and 100 fathoms (2 lots); 3½ miles N.E. off Pacific Reef, Key Largo in 66 fathoms.

Dentalium (Bathoxiphus) didymum Watson

Dentalium didymum WATSON 1879, J. Linn. Soc. London **14,** p. 517; WATSON 1885, *Challenger* Rept. Zoöl. **15,** p. 10. pl. 1, fig. 11; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 83, pl. 14, fig. 10.

Notes. Dr. WILLIAM J. CLENCH obtained a large series of *Dentalium* from the channel dredgings at Puerto Plata Harbor, Santo Domingo. Among them were a number of fragments and a few nearly complete specimens of this very rare species. They were taken from a fine grey mud brought up from a depth of 20 to 30 feet. A single specimen was found in a lot of *Blake* material from off Tortugas.

Records. FLORIDA: *Blake*, station 43, from south of Dry Tortugas (N. Lat. 24° 08′; W. Long. 82° 15′) in 33 fathoms. HISPANIOLA: Puerto Plata Harbor, Santo Domingo in 20 to 30 feet.

Entalina platamodes Watson

Siphodentalium platamodes WATSON 1879, J. Linn. Soc. London **14,** p. 519; WATSON 1885, *Challenger* Rept., Zoöl. **15,** p. 13, pl. 2, fig. 4.

Entalina platamodes PILSBRY and SHARP 1897, Manual of Conchology (1) **17,** p. 133, pl. 23, fig. 3–5; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 87, pl. 15, figs. 1, 4, 5, 7.

Entalina quadrata HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 88, pl. 15, figs. 2, 3, 6, 10.

Notes. A lot of four specimens of this apparently rare species was taken by the *Atlantis*. HENDERSON records three specimens from two localities off the coast of Florida and his *quadrata* was repesented by a single specimen from off Grenada, Lesser Antilles. EMERSON reported five lots from off Puerto Rico totaling some 200 specimens which would indicate that in some localities at least they may be quite common. This is the first record for Cuba.

Records. Atlantis, station 2989, off Puerto Sagua la Grande, Oriente (N. Lat. 23° 10′; W. Long. 80° 04′) in 360 fathoms.

Cadulus (Polyschides) tetraschistus Watson

Siphodentalium tetraschistum WATSON 1879, J. Linn. Soc. London **14,** p. 521; WATSON 1885, *Challenger* Rept. Zoöl. **15,** p. 15, pl. 2, fig. 8.

Cadulus (*Polyschides*) *tetrachistus* [sic] Watson, HENDERSON 1920, Bull. U. S. Nat. Mus. No. 111, p. 97, pl. 17, fig. 1.

Notes. Two lots of this species are in the collection of the Museum of Comparative Zoölogy. I agree with HENDERSON that this South American species appears to be distinct from *quadridentatus* Dall. It is a slightly shorter, stouter species with a more solid shell. The apical lobes are shorter with broader clefts between them. The shell surface has a slight chalky texture and is marked by distinct opaque white rings. In *quadridentatus* the shell is very shiny, a clear translucent blue-white, and in perfect specimens the apical lobes are long, straight sided and with very narrow clefts between them. The only other known record is from Fernando Noronha in 25 fathoms, collected by the *Challenger*.

Records. URUGUAY: off Montevideo (S. Lat. 35° 12′, 15″; W. Long. 55° 30′) in 7 fathoms (*Hassler* Exped.) ARGENTINA: Puerto Quequen, Buenos Aires.

Cadulus (Polyschides) quadridentatus Dall

Siphonodentalium quadridentatum DALL 1881, Bull. Mus. Comp. Zoöl. **9**, p. 36.

Cadulus quadridentatus DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 428, pl. 27, fig. 5; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 97, pl. 17, fig. 2–3.

Notes. Three new records for this rather common and characteristic species are added.

Records. FLORIDA: 18 miles S by W of Destin in 18–20 fathoms (T. MCGINTY). CUBA: La Chorrera, Habana. BERMUDA (O. BRYANT).

Cadulus (Polyschides) tetrodon Pilsbry and Sharp

Cadulus (*Polyschides*) *tetrodon* PILSBRY and SHARP 1897, Manual of Conchology (1) **17**, p. 151, pl. 29, figs. 14–18; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 101, pl. 17, fig. 5.

Notes. The lot from off Carysfort Light in 100 fathoms makes a new depth record for this species.

Records. FLORIDA: Boynton Beach in 40 feet (T. MCGINTY); 4 mi. N.E. of Beacon D, Key Largo in 66 fathoms; 5 mi. N.E. of Carysfort Light, Key Largo in 100 fathoms (both L. A. BURRY).

Cadulus (Polyschides) carolinensis Bush

Cadulus carolinensis BUSH 1885, Trans. Connecticut Acad. Arts and Sci. **6**, p. 471, pl. 45, fig. 19; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 102, pl. 17, figs. 6–7.

Notes. This is a very common species in the region of Cape Hatteras, North Carolina, but records from Florida, particularly the west coast, are rare.

Records. FLORIDA: 15–35 miles off Fort Walton in 13–20 fathoms (L. A. BURRY, 2 lots).

Cadulus (Platyschides) grandis Verrill

Cadulus grandis VERRILL 1884, Trans. Connecticut Acad. Arts and Sci. **6**, pt. 1, p. 219; pt. 2, pl. 44, fig 20; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 105, pl. 17, fig. 12.

Notes. Three lots of this large and common *Cadulus* were taken by the *Atlantis*.

Records. NEW JERSEY: *Atlantis* station (N. Lat. 39° 40′; W. Long. 71° 43′) in 820 fathoms; *Atlantis* station (N. Lat. 39° 34′; W. Long. 71° 44′) in 935 fathoms, both about 120 miles E. of Great Bay. VIRGINIA: *Atlantis* station about 80 miles N.E. of Cape Charles (N. Lat. 37° 21′; W. Long. 74° 12′) in 860 fathoms.

Cadulus (Platyschides) agassizii Dall

Cadulus agassizii DALL 1881, Bull. Mus. Comp. Zoöl. **9**, p. 35; DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 430; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 110, pl. 18, figs. 1, 3.

Notes. Only a single new record for this rather common species is added. The species ranges from off Chesapeake Bay south to Key West, Florida, and HENDERSON records large series from off Fowey Light and Sand Key Florida.

Records. FLORIDA: *Bibb* station 179, off Tennessee Reef (N. Lat. 24° 35′ 00″; W. Long. 80 39′ 00″) in 115 fathoms.

Cadulus (Platyschides) watsoni Dall

Cadulus watsoni DALL 1881, Bull. Mus. Comp. Zoöl. **9**, p. 34; DALL 1889, Bull. Mus. Comp. Zoöl. **18**, p. 429, pl. 27, fig. 12a; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 120, pl. 18, fig. 12.

Notes. A large fine specimen of this very rare species was taken by the *Atlantis*; this is the third known record. The original lot was taken off Cape San Antonio, Cuba, and a second lot of five specimens in the United States National Museum is from off Old Providence Island, Caribbean Islands.

Records. CUBA: *Atlantis*, station 2989, off Sagua la Grande, Las Villas (N. Lat. 23 10′; W. Long. 80° 04′) in 360 fathoms.

Cadulus (Platyschides) elongatus Henderson

Cadulus (*Platyschides*?) *elongatus* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 122, pl. 19, fig. 15.

Notes. This species was described by Henderson from a unique specimen dredged off the mouth of the Mississippi River in 68 fathoms. A series of five specimens and a number of fragments was obtained by Mrs. L. A. Weisenhaus by washing the mud from a shrimp boat net and anchor. The specimens agree well with Henderson's description.

Records. TEXAS: off Port Isabel in 50 fathoms.

Cadulus (Platyschides) braziliensis Henderson

Cadulus (*Platyschides*) *braziliensis* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 124, pl. 19, fig. 16.

Notes. The single specimen dredged by the *Hassler* makes the second known record for this species. Henderson described the species from a lot of two specimens dredged by the *Albatross* off Rio de Janeiro, Brazil. This coast is so poorly known that the few records available are no indication of the abundance or distribution of the species.

Records. URUGUAY: off Montevideo (S. Lat. 35° 12′; W. Long. 55° 30′) in 7 fathoms (*Hassler* Exped.).

Cadulus (Platyschides) simpsoni Henderson

Cadulus (*Platyschides*) *simpsoni* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 127, pl. 19, fig. 17.

Notes. The *Atlantis* obtained two lots of this species, bringing the known records up to five. It is probably not a rare species, however, to judge by the size of some of the lots.

Records. CUBA: *Atlantis* station 2987E, off Sagua la Grande, Las Villas (N. Lat. 23° 19′; W. Long. 79° 59′) in 315 fathoms; *Atlantis*, station 2963, off Bahía Cochinos, Las Villas (N. Lat. 22° 07′; W. Long. 81° 08′) in 180–190 fathoms.

Cadulus (Gadila) mayori Henderson

Cadulus (*Gadila*) *mayori* Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 133, pl. 19, fig. 3.

Notes. Like *Cadulus elongatus* this species was obtained by Mrs. Weisenhaus from the mud on the net and anchor of a shrimp boat. The records from Cuba are the first for that island.

Records. FLORIDA: 2½ miles S.S.E. of Looe Key, Marathon in 50 fathoms; 5 miles E. of Carysfort Light in 96–107 fathoms (both L. A. Burry). TEXAS: off Port Isabel in 50 fathoms. CUBA: *Blake*, station 20, off Bahia Honda (N. Lat. 23° 02′; W. Long. 83° 11′) in 220 fathoms; *Atlantis*, station 2981C, off Punta Alegre, Camagüey (N. Lat. 22° 47′; W. Long. 78° 49′) in 195 fathoms; *Atlantis*, station 2963, off Bahía Cochinos, Las Villas (N. Lat. 22° 07′; W. Long. 81° 08′) in 180–190 fathoms.

Cadulus (Gadila) acus Dall

Cadulus acus Dall 1889, **Bull.** Mus. Comp. Zoöl. **18**, p. 432, pl. 27, fig. 11.

Cadulus (*Gadila*) *acus* Dall, Henderson 1920, Bull. U.S. Nat. Mus. No. 111, p. 140, pl. 20, figs. 11, 13.

Cadulus (*Gadilopsis*) *acus* Dall, Emerson 1952, Smithsonian Misc. Coll. **117**, No. 6, p. 10.

Notes. A very large lot of 250 or more specimens was collected by Dr. Clench from a fine grey mud brought up during the channel dredging operations in Puerto Plata Harbor, Santo Domingo.

Records. CUBA: La Chorrera, Habana. HISPANIOLA: Puerto Plata Harbor, Santo Domingo. VIRGIN ISLANDS: St. Thomas.

Cadulus (Gadila) verrilli Henderson

Cadulus (*Gadila*) *verrilli* HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 136, pl. 19, fig. 13.

Notes. HENDERSON records only four lots of this species, all from off Martha's Vineyard, Mass.

Records. RHODE ISLAND: 76 miles south of Block Island in 180–190 fathoms (J. MILLER).

Cadulus (Cadulus) ampullaceus Watson

Cadulus ampullaceus WATSON 1879, J. Linn. Soc. London **14**, p. 529; WATSON 1885, *Challenger* Rept., Zoöl. **15**, p. 23, pl. 3, fig. 11; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 144, pl. 19, fig. 7.

Notes. Two lots that are referable to this minute but characteristic species were collected by the *Atlantis*. The only other known lot is that taken by the *Challenger* off Culebra Island.

Records. CUBA: *Atlantis*, station 2961C, off Bahía Cochinos (N. Lat. 22° 07′; W. Long. 81° 08′) in 190–370 fathoms; *Atlantis*, station 2967B, off Guantanamo Bay, Oriente (N. Lat. 19° 43′; W. Long. 74° 57′ 30″) in 1330–1650 fathoms.

Cadulus (Cadulus) exiguus Watson

Cadulus exiguus WATSON 1879, J. Linn. Soc. London **14**, p. 528; WATSON 1885, *Challenger* Rept., Zoöl. **15**, p. 23, pl. 3, fig. 10; HENDERSON 1920, Bull. U.S. Nat. Mus. No. 111, p. 145, pl. 20, fig.9.

Notes. This is the seventh known record for this species. It has been recorded from Culebra Island, Barbados; from three stations off Puerto Rico, and one from the " Bahamas ". This is the first record for Cuba, and the specimens were dredged from a much greater depth than any previous lots.

Records. CUBA: *Atlantis*, station 2959, off the Isle of Pines (N. Lat. 21° 17′; W. Long. 83° 06′) in 2050 fathoms.

CATALOGUE OF THE SCAPHOPOD TYPES IN THE MUSEUM OF COMPARATIVE ZOOLOGY

In the following catalogue of the types it will be noted that the holotypes of many of the species that DALL described in the " Blake Report " are in the Museum of Comparative Zoology. It is difficult to know just what HENDERSON (1920) meant by his use of the word " Type ". If he was referring to the holotype, he made some rather curious errors. He was probably using it to refer to any of the primary types, for indeed all his references are to either holotypes or paratypes. It is curious that he says, under *Cadulus aequalis* Dall " The type Cat. No. 95373, U.S.N.M. is from a lot of two specimens taken by the *Blake* . . ." and later " This is the unique museum record ", when, in the original description, DALL stated that he had three specimens. This third specimen was the one selected by DALL as the holotype and returned to the Museum of Comparative Zoology. Though HENDERSON says in the introduction to his paper that he had the entire collection from the Museum of Comparative Zoology for study, one wonders if he actually did. In any event, he put very little of this material on record.

acus Dall *Cadulus* 1889, Bull. Mus. Comp. Zoöl. **18**, p. 432, pl. 27, fig. 11. Holotype, MCZ 7751 Samana Bay, Santo Domingo in 16 fathoms. This is the specimen figured by DALL and was so labelled by him.

aequalis Dall, *Cadulus* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 34; DALL 1889, Bull. Mus. Comp. Zoöl. **18,** p. 429, pl. 27, fig. 9. Holotype, MCZ 7740, *Blake*, station 43, from off Tortugas, Florida (N. Lat. 24° 08′; W. Long. 82° 51′) in 339 fathoms. This is the specimen figured by DALL.

agassizii Dall, *Cadulus* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 35; DALL 1889, Bull. Mus. Comp. Zoöl. **18,** p. 430, pl. 27, fig. 12c. Holotype, MCZ 7746, *Blake*, station 5, from south of Marquesas Keys, Florida (N. Lat. 24° 05′; W. Long. 82° 13′) in 229 fathoms. This is the specimen figured by DALL.

amiantus Dall, *Cadulus* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 431, pl. 27, fig. 7. Holotype, MCZ 7749, *Blake*, station 19, from off Bahía Honda, Pinar del Río, Cuba (N. Lat. 23° 03′ 00″; W. Long. 83° 10′ 30″) in 310 fathoms.

atlanticus Henderson *Cadulus* (*Gadila*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 137, pl. 20, fig. 2. Paratype, MCZ 186815, from U.S.B.F. *Albatross* station 2862, from off Nantucket Island, Mass. (N. Lat. 39° 38′ 00″; W. Long. 70° 22′ 00″) in 1004 fathoms.

barbadensis Henderson *Cadulus* (*Cadulus*) *transitorius* 1920, Bull. U.S. Nat. Mus. No. 111, p. 144, pl. 19, fig. 7. Paratype MCZ 7744, *Blake*, station without number, from off the Barbados in 100 fathoms. This specimen was labelled as type by HENDERSON though curiously he does not mention the specimen in his paper.

bushii Dall *Cadulus* (*carolinensis* var.?) 1889, Bull. Mus. Comp. Zoöl. **18,** p. 430, not figured. Holotype MCZ 7745, *Blake*, station from off Barbados in 100 fathoms. This is the specimen measured by DALL and returned to the Museum of Comparative Zoology.

bushi Henderson *Siphonodentalium* (*Pulsellum*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 94, pl. 16, fig. 6. Paratype MCZ 186822, *Albatross* station 2710, off [Barnegat Bay], New Jersey (N. Lat. 40° 06′ 00″; W. Long. 68° 01′ 30″) in 984 fathoms.

callipeplum Dall, *Dentalium* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 419, pl. 27, fig. 12b. Holotype MCZ 7672, *Blake*, station 167, from off Guadeloupe, Lesser Antilles (N. Lat. 16° 09′; W. Long. 61° 29′) in 175 fathoms. This is the specimen figured by DALL and so labelled by him. It even shows the hole in the side which is indicated in the figure. The type locality is that given above rather than U.S.B.F. station 2400, between the Mississippi River delta and Cedar Keys in 169 fathoms as given by HENDERSON.

callithrix Dall *Dentalium* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 427, pl. 27, fig. 10. Holotype MCZ 7734, *Blake*, station 236, off Bequia, Grenadines (N. Lat. 12° 52′; W. Long. 61° 96′) in 1591 fathoms. This is the specimen labelled by DALL as ‘ Figured type ’ and is the one figured in the *Blake* Report. HENDERSON reports the type as from a *Blake* station, in Yucatan Straits in 640 fathoms.

carduus Dall, *Dentalium* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 423, pl. 27, fig. 3. Holotype MCZ 7692, *Blake*, station 220, off St. Lucia, Lesser Antilles (N. Lat. 13° 50′; W. Long. 61° 03′) in 116 fathoms. This is the figured specimen.

carolinensis Bush, *Cadulus* 1885, Ann. Report of the Commissioner of Fish and Fisheries for 1883, p. 587; BUSH 1885, Trans. Connecticut Acad. Arts and Sci. **6,** pt. 2, p. 471, pl. 45, fig. 19. Paratypes MCZ 186818, *Albatross*, station 2114, off Cape Hatteras, North Carolina (N. Lat. 35° 20′ 00″; W. Long. 75° 20′ 00″) in 14 fathoms.

ceratum Dall *Dentalium* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 38; DALL 1889, Bull. Mus. Comp. Zoöl. **18,** p. 424, pl. 26, fig. 5, pl. 27, fig. 2. Paratype MCZ 7697, *Blake*, station 2, off Habana, Cuba (N. Lat. 23° 14′; W. Long. 82° 25′) in 805 fathoms.

cucurbita Dall *Cadulus* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 35; DALL 1889, Bull. Mus. Comp. Zoöl. **18,** p. 431, pl. 27, fig. 12d. Holotype MCZ 7750, *Blake*, station 19, off Bahía Honda, (Pinar del Río) Cuba in 310 fathoms.

elephas Henderson *Cadulus* (*Platyschides*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 107, pl. 17, fig. 10. Holotype MCZ 7741, *Blake*, station 230, off St. Vincent, Lesser Antilles (N. Lat. 13° 13′ 20″; W. Long. 61° 18′ 45″) in 464 fathoms.

gouldii Dall *Dentalium* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 424 (not figured). Paratype MCZ 7707, *Blake*, station 65, off Habana, Cuba in 127 fathoms. This was a poor and badly worn specimen. Better specimens were obtained off the Barbados at *Blake* station 299 in 140 fathoms along with *obscurum Dall.*

grandis Verrill *Cadulus* 1884, Trans. Connecticut Acad. Arts and Sci. **6,** pt. 1, p. 219; **6,** pt. 2, pl. 44, fig. 20. Paratype MCZ 186804, *Albatross*, station 2076, about 230 miles E. of Martha's Vineyard, Massachusetts (N. Lat. 41° 13′ 00″; W. Long. 66° 00′ 50″) in 906 fathoms.

lunula Dall *Cadulus* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 35; Dall 1889, Bull. Mus. Comp. Zoöl. **18,** p. 431, pl. 27, fig. 8. Holotype MCZ 7747, *Blake*, station 2, off Morro Light, Habana, Cuba in 805 fathoms.

mayori Henderson *Cadulus* (*Gadila*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 133, pl. 19, fig. 3. Paratype MCZ 48411, *Eolis*, station 43, off Key West, Florida in 63 fathoms.

miamiensis Henderson *Cadulus* (*Platyschides*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 129, pl. 19, fig. 18. Paratype MCZ 48413, *Eolis*, station 348, off Fowey Light, Florida in 110 fathoms.

nanus Clench and Aguayo *Cadulus iota* 1939, Mem. de la Soc. Cubana de Hist. Nat. **13,** No. 3, p. 197. Holotype MCZ 89222, Gibara, Oriente Province, Cuba in 40 fathoms.

obscurum Dall *Dentalium gouldii* var. 1889, Bull. Mus. Comp. Zoöl. **18,** p. 424, pl. 27, fig. 4 (not pl. 26 as given in the text). Holotype MCZ 7708, *Blake*, station 299, off Barbados, Lesser Antilles (N. Lat. 13° 05′ 00″; W. Long. 59° 39′ 40″) in 140 fathoms. This is the specimen figured by Dall and so labelled by him, [not station 229 as given by Henderson.]

occidentale Henderson, *Siphonodentalium* (*Pulsellum*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 93, pl. 16, fig. 4. Paratype MCZ 186823, from U.S.B.F. *Fish Hawk*, station 871, off Martha's Vineyard, Massachusetts (N. Lat. 40° 02′ 54″; W. Long. 70° 23′ 40″) in 115 fathoms. Henderson records 86 fathoms for this station in his original description, but the station lists give 115.

ophiodon Dall *Dentalium* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 38; Dall 1889, Bull. Mus. Comp. Zoöl. **18,** p. 427, pl. 26, fig. 9. Paratype MCZ 7729, *Blake*, station 21, off Bahía Honda (Pinar del Río) Cuba in 827 fathoms.

pandionis Verrill and Smith *Cadulus* 1880, Amer. J. Sci. **20,** p. 399. Paratypes MCZ 186811, *Fish Hawk*, station 877, south of Marthas Vineyard, Massachusetts (N. Lat. 39° 56′; W. Long. 70° 54′ 18″) in 126 fathoms.

parvus Henderson *Cadulus* (*Platyschides*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 113, pl. 18, figs. 2, 4. Paratypes MCZ 48414, State Univ. of Iowa, station 44 off the Barbados, Lesser Antilles in 90 fathoms.

perlongum Dall *Dentalium* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 36; Dall 1889, Bull. Mus. Comp. Zoöl. **18,** p. 419, pl. 27, fig. 6. Holotype MCZ 7752, *Blake*, station 33 from north of the Yucatan Bank (N. Lat. 24° 01′; W. Long. 88° 58′) in 1568 fathoms. This specimen is the only one in the four lots mentioned by Dall in his original description that measures 80 mm and agrees with his figure. Consequently, though Dall did not label it as the figured specimen, there seems no question but that it is the holotype. Henderson states that " the type is not in the United States National Museum ".

poculum Dall *Cadulus* 1889, Bull. Mus. Comp. Zoöl. **18,** p. 429 (not figured). Holotype MCZ 7743, *Blake* station, off Cape San Antonio, Cuba [Yucatan Strait] in 640 fathoms. Dall did not figure this species but the specimen which he measured, the largest of those obtained, is in the MCZ collection.

quadridentatus Dall *Siphonodentalium* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 36; Dall 1889 *Cadulus quadridentatus*, Bull. Mus. Comp. Zoöl. **18,** p. 428, pl. 27, fig. 5. Holotype MCZ 7739, Pourtalès dredgings on the west coast of Florida in 30 fathoms.

sigsbeanum Dall *Dentalium* 1881, Bull. Mus. Comp. Zoöl. **9,** p. 38. Holotype MCZ 7737, *Blake*, station from Yucatan Strait in 640 fathoms.

spectabilis Verrill *Cadulus* 1885, Trans. Connecticut Acad. Arts and Sci. **6**, pt. 2, p. 432, pl. 44, fig. 19. Paratype MCZ 186801, *Albatross*, station 2221, about 180 miles off Ocean City, New Jersey (N. Lat. 39° 05′ 30″; W. Long. 70° 44′ 30″) in 1525 fathoms. Henderson was in error when he stated that the type of this species was from U.S.B.F. station 2711. This station was not included in Verrill's original description, and in fact station 2711 was made on September 16, 1886, and Verrill's description was published in June 1885. The holotype is in the U.S. Nat. Mus. No. 40,498 from station 2221.

taphrium Dall *Dentalium* 1889, Bull. Mus. Comp. Zoöl. **18**, p. 422, (not figured). Paratype MCZ 7690 from off the Carolina Coast in 52 fathoms.

watsoni Dall *Cadulus* 1881, Bull. Mus. Comp. Zoöl. **9**, p. 34; Dall 1889, Bull. Mus. Comp. Zoöl. **18**, p. 429, pl. 27, fig. 12a. Holotype MCZ 7742 from *Blake*, station off Cape San Antonio, Cuba in 413 fathoms.

verrilli Henderson *Cadulus* (*Gadila*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 136, pl. 19, fig. 13. Paratype MCZ 186819 U.S.B.F. *Fish Hawk*, station 871, off Martha's Vineyard, Massachusetts (N. Lat. 40° 02′ 54″; W. Long. 70° 23′ 40″) in 115 fathoms.

verrilli Henderson *Siphonodentalium* (*Siphonodentalium*) 1920, Bull. U.S. Nat. Mus. No. 111, p. 91, pl. 16, figs. 2 and 7. Paratype MCZ 186821 from *Albatross*, station 2710, off Nantucket (N. Lat. 40° 06′ 00″; W. Long. 68° 01′ 30″) in 984 fathoms.

REFERENCES

Chace, F. A. (1940), The *Atlantis* Expedition to the West Indies in 1938 and 1939, under the joint auspices of the University of Havana and Harvard University. List of Stations. *Woods Hole Oceanogr. Inst. Contrib.* No. 274, 1–8.

Dall, W. H. (1881), Reports on the Results of Dredging under the supervision of Alexander Agassiz —by the coast survey Steamer *Blake*. Preliminary Report on the Mollusca. *Bull. Mus. Comp. Zoöl.* **9**, (2), 33–39.

Dall, W. H. (1895), Reports on the Results of Dredging, etc. by the *Blake*. Report on the Mollusca Part 2, Gastropoda and Scaphopoda. *Bull. Mus. Comp. Zoöl.* **18**, 418-432, pls. 26–27.

Emerson, W. K. (1952), The Scaphopod Mollusks collected by the First Johnson-Smithsonian Deep-Sea Expedition. *Smithsonian Misc. Coll.* **117** (6), 1–14.

Henderson, J. B. (1920), A Monograph of the East American Scaphopod Mollusks. *Bull. U.S. Nat. Mus.* No. 111, 1–177, pls. 1–20.

Pilsbry, H. A. and Sharp, B. (1897), Scaphopoda. Manual of Conchology (1) **17**, 1–280, pls. 1–37.

Watson, R. B. (1885), *Scaphoda*, *Repts. Sci. Res.*, H.M.S. *Challenger*, *Zool.* **15**, 1–24, pls. 1–3.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 321-330.

Effect of freshets on Passamaquoddy plankton

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Summary—Sudden or heavy discharge into Passamaquoddy Bay, from streams at its head, works out through the 10-mile long Bay and through the 8-mile long Head Harbour Passage, its main connection with the Bay of Fundy, in less than 10 days, as shown by the salinity of the water. Through the Bay, the outflow is more or less superficial and carries certain elements of the plankton out into the Passage. But, in the latter, strong tidal mixing prevents stratification, although the water is deeper. Under these circumstances, working of the freshet outward has a double effect, first a carrying out of the well-mixed plankton, and then an indraft of deep plankton from without. The latter provides an abundance of planktonic animals in the Passage at all depths.

FORTY YEARS ago, Dr. JOHAN HJORT, of Norway, brought HENRY B. BIGELOW and me together in the expedition (HJORT, 1919), which he was organizing for the Biological Board of Canada. It was for me a marvellous introduction to the oceanographic problem in our waters. The methods used were those with which HJORT had been concerned in north European waters and BIGELOW in waters off the New England and Nova Scotian coasts. In the picture that was developed, the Bay of Fundy, which I was investigating for quite a few years from the Atlantic Biological Station at St. Andrews, New Brunswick, stands out like a sore thumb, in the peculiarity of both its plankton and its hydrography. This is in association with very heavy tidal action. There is also a striking peculiarity in the wealth of fish as well as of zooplankton near the surface in the Passamaquoddy region near the mouth of the Bay (HUNTSMAN, 1927). When the Passamaquoddy Power Project made the explanation of this condition desirable, BIGELOW asked me whether temperature explained this, and, if not, what could the explanation be. This paper gives part of the answer to his question and is offered as a tribute to the stimulating effects of long and most enjoyable association with him in oceanographic investigations.

The herring is by far the most abundant fish in the Passamaquoddy region (Fig. 1). Its food consists mainly of Crustacean zooplanktons of the orders Copepoda and Euphausiacea, which are known to the local fishermen as " red feed " and " shrimp " respectively, as seen in herring stomachs. The distribution of such zooplankton both vertically and horizontally determines its availability to the herring, which take these forms individually as silhouetted against the sky when a matter of inches above them. The herring have their own peculiar vertical and horizontal distribution, and vary in condition in accordance with the food available at the place and the time (BATTLE, *et al.*, 1936). Freshets in the rivers that discharge into Passamaquoddy Bay shift the herring about from one place to another (HUNTSMAN, 1934), as do other factors that bring about movements of the water. Also, mixture over shoals under tidal action of the water of this Bay, which is stratified from river discharge, concentrates the herring and their planktonic food together for effective feeding (BATTLE, *et al.*, 1936). There has been need for elucidation of any effects of freshets in shifting the zooplankton from place to place.

ESTUARIAL CIRCULATION OF ZOOPLANKTON

The typical circulation of water in a river estuary is movement oceanward of the fresher and lighter surface water, and movement riverward of the salter and heavier deeper water. This is dependent upon tidal mixing of the fresh river water with the salt sea water. It will depend upon the depth from the surface to which particular

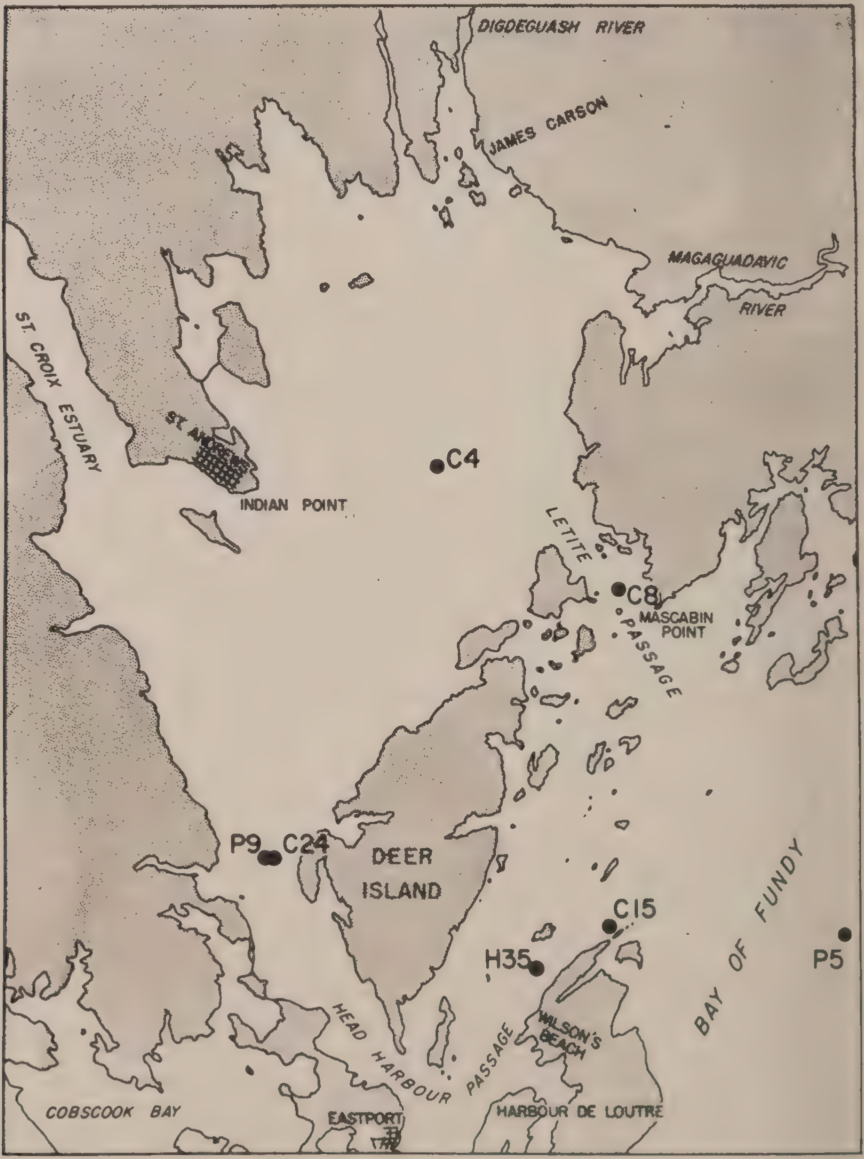
DIGDEGUASH RIVER
JAMES CARSON
MAGAGUADAVIC RIVER
ST. CROIX ESTUARY
ST. ANDREWS
INDIAN POINT
C4
LETITE PASSAGE
C8
MASCABIN POINT
P9
C24
DEER ISLAND
C15
H35
P5
BAY OF FUNDY
HEAD HARBOUR PASSAGE
WILSON'S BEACH
COBSCOOK BAY
EASTPORT
HARBOUR DE LOUTRE

Fig. 1. Passamaquoddy Bay, New Brunswick, showing principal rivers, passages to Bay of Fundy and positions of the stations mentioned.

zooplanktonts keep, and upon the depths of the two movements, as to whether these will be carried oceanward out of the estuary or riverward to be concentrated at the head of the estuary. The strengths and depths of the movements will depend, not only upon the degree of tidal mixing, but also upon the amount of river water. Any estuarial concentration of zooplankton there may be, will be increased by freshets in the river.

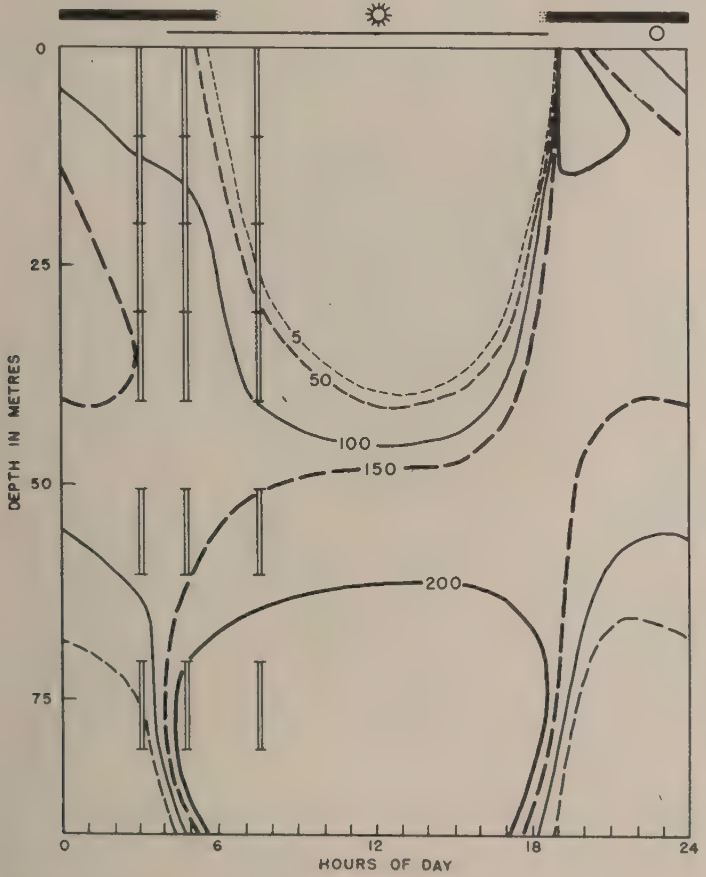

Fig. 2. Vertical distribution of *Calanus* throughout the 24-hr. day at Prince station No. 5 in the Bay of Fundy, as inferred from vertical tows made on September 20, 1926, through ten metres of water at different depths on three occasions: (1) between 2.50 and 3.55 hr., (2) between 4.35 and 5.25 hr. and (3) between 7.15 and 7.55 hr., as shown by vertical lines. Periods of sunlight and moonlight are shown at the top, and numbers of *Calanus* are per tow.

While the zooplanktonts may be at the proper depth during the day for transport riverward, their migration towards the surface at night may well result in their being carried oceanward. So complex is the situation that, as yet, only their actual distribution can be depended upon to show in which direction particular zooplanktonts have moved.

DIURNAL MIGRATION OF *CALANUS*

The principal zooplanktont for food of Passamaquoddy herring is the copepod, *Calanus finmarchicus*. Its vertical migrations are so complex (ESTERLY, 1919; RUSSELL, 1926; CLARKE, 1933; and CUSHING, 1951) that local and temporal data seem necessary to show its vertical distribution that may determine how it will be shifted in the Passamaquoddy circulation. Fig. 2 gives an interpretation of the vertical distribution of this species throughout an entire day at Prince Station No. 5, in water about 90 metres deep in the Bay of Fundy just outside the main passage leading to Passamaquoddy Bay. It is believed that this is sufficiently representative of the times and places dealt with, except as altered by vertical movements of the water. The interpretation is based, as shown, mainly upon data obtained on September 20, 1926, in closing vertical tows through six different strata at three different times with rapidly increasing light intensity in the morning. It will be evident that these copepods were on the whole more heavily concentrated near the bottom, and least heavily near the surface.

CHARACTERISTICS OF THE REGION

Passamaquoddy Bay (Fig. 1) is about five miles wide and ten miles long. On its east side, it is connected with the Bay of Fundy through the relatively short and shallow Letite Passage, and also through the still shallower Little Letite Passage. The main connection, however, is at the south end through the long and tortuous, as well as deep, Western or Head Harbour Passage (also called " Quoddy River "), which virtually forms its mouth. The Passages have very rough, irregular and rocky bottom. The Bay inside is of rather uniform depth, from 20 to 35 metres, but it is still deeper near the Passages.

Fresh water is discharged into the Bay mainly from the St. Croix, Magaguadavic and Digdeguash Rivers. The St. Croix River discharges into the west side of the Bay near its mouth somewhat more than 2,000 sec/ft from a drainage basin of over 1,300 square miles. It is controlled for power purposes, so that in summer the discharge is comparatively steady, ranging for the most part from 500 to 2,000 sec/ft. The Magaguadavic River discharges on the average around 1,000 sec/ft from more than 600 square miles into the Bay on its east side near its head, and it is similarly controlled for power purposes. The Digdeguash River, together with other uncontrolled streams, discharges into the head of the Bay the drainage from about 300 square miles. The volume and availability of this discharge may be judged from records made on the Magaguadavic River at Elmcroft (above the level of storage) with a drainage area of about 350 square miles. From 2 to 6 inches of rain fell over the drainage basin on August 26 and 27, 1924, and the rates of discharge on successive days, beginning on August 25, were: 85; 246; 2,890; 2,520; 2,030; 518; 339; 276 sec ft. Therefore, with heavy rains, the principal increase in river discharge is a day or so after the rain. With other rivers controlled, this is into the head of the Bay. It is to be noted that the discharges of the St. Croix and Magaguadavic Rivers reach the Bay only after having been mixed with sea water in estuaries, which are fifteen and four miles long respectively. The estuary of the Digdeguash River is about two miles long.

The tides of the region are very heavy, the amplitude ranging from 20 to 25 feet. The rough character of the bottom near shore and in the Passages makes the strong tidal currents very effective in mixing the light river water with the heavy sea water. This is evident for the Bay itself in that near the mouth the salinities at the surface and at 50 metres depth, which is deeper than the Bay in general, were for example on October 12, 1933: 30·99 and 31·73°/$_{oo}$ respectively. Also, the salinities at the same depths on the same day at Station No. 5 outside Head Harbour Passage were: 31·98 and 32·32°/$_{oo}$ respectively. KETCHUM and KEEN (1953) have calculated that in August of 1951 the mixed water moving out of the Bay near its mouth was over 100 times as great as that of the discharge from rivers, and that outside the Passages it had increased to nearly 600 times.

Owing to their shallowness, the Letite Passages do not permit much movement of water through, so that the principal outlet for mixed water and the principal inlet for salt water is Head Harbour Passage. Also, movement through the Letite Passages is more inward than outward, as determined through a complete tidal cycle in 1951. But, there is very definite passage out of mixed water through Letite and passage in of salt water, as well as very heavy mixing of the two.

RAINFALL AND PLANKTON INDRAFT

Calanus is not produced to any particular extent in the Passamaquoddy region, but is there as an immigrant from the Gulf of Maine (WRIGHT, 1929; FISH, 1936). It was very abundant at Prince Station No. 5 just outside Passamaquoddy Bay in the late summer of 1933. Vertical hauls with the No. 0 (bolting cloth measure) net from 90 to 0 metres gave the following quantities in cubic centimetres of settled plankton (chiefly *Calanus*) on the dates indicated: 13 on July 10; 9 on August 11; 22 on September 15.

The quantity of *Calanus* at Station No. 5 varied greatly from September 23 to October 3. Deep tows were made on the former date, giving large quantities at from 100 to 50 metres and at about 90 metres. On October 2, a vertical haul gave only 2 cu.cm. Yet, deep tows made the next day revealed even greater abundance than on September 23.

During the night of September 17–18 there was a very heavy rainfall over the basin that drains into the head of Passamaquoddy Bay, over 5 in. falling at St. Andrews and 4·81 in. at St. George on west and east sides of the Bay, and 3·25 in. at McAdam at the head of the drainage into the Digdeguash River. Three days later, another inch of rain fell over the area. It is estimated that these rainfalls more than doubled the amount of fresh water being discharged into the Bay.

KETCHUM and KEEN (1953) have calculated that the mean flushing time for the removal from Passamaquoddy Bay of fresh water discharged into it is 15·8 days, and they conclude that " it seems probable that a flushing time of about 15 days should be approximately correct ". In late summer of 1933, there were three heavy rainfalls recorded, on August 25, September 18 and October 7. Weekly determinations of bottom salinity in the middle of Passamaquoddy Bay showed that higher salinity returned between 5 and 13, 9 and 16, and 11 and 18 days respectively. If such return has a constant period, it will, therefore, lie between 11 and 13 days after the rainfall. After the freshet of September 18, salinities were measured for Prince Station No. 9, which is off Clam Cove Head at the mouth of Passamaquoddy Bay where it joins Head Harbour Passage, on September 23, 26 and 29, and on October 3. The values at 50 metres depth were 31·78°/$_{oo}$, 31·67°/$_{oo}$, 31·85°/$_{oo}$ and 31·89°/$_{oo}$ respectively. This shows that salter water was entering the mouth of the Bay 11 days after the rainfall. What relation this has to the flushing time is not clear. It may represent merely the beginning of heavy interchange at the mouth of the large mass of fresh water.

In Head Harbour Passage, particularly the outer part, heavy tidal action and irregular bottom keep the water quite thoroughly stirred, so that the plankton present can easily be obtained in tows at any depth. Tows were made at two Stations (H.F. 50 and 35) in the outer part of the Passage on September 18 (at 50 only), 23, 26, 29 and October 3. The quantities (cu.cm. after settling) of plankton (chiefly *Calanus*) were: 12; 8 and 16; 18 and 12; 180 and 95; and 80 and 27 respectively. There was thus a very marked increase in quantity between 8 and 11 days after the rainfall. It would seem to be possibly significant that, following the heavy indraft of *Calanus* into the Passage, as found on September 29, there was a low amount outside on October 2, but not on October 3. The movement outward of the mixed water from the freshet might be expected to have such temporary effect in carrying outward much of the plankton.

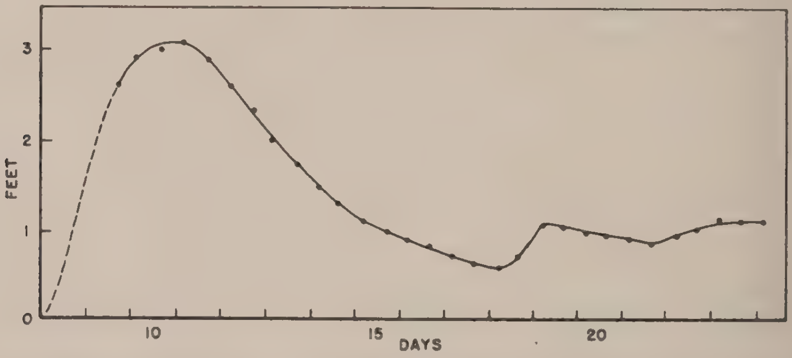

Fig. 3. Height above low water of surface of Digdeguash River at the Stillwater bridge in August, 1951.

The very definite result was that a dearth of *Calanus* in Head Harbour Passage was changed to abundance when the water from the freshet worked its way out. *Calanus* had been abundant in deep water outside, but the freshet made it abundantly available to birds and to herring and other near-surface fishes by bringing it into the Passage, where vertical currents lift it rather steadily toward the surface, overcoming its tendency to descend from daylight. As far as the facts went, this was coincident with entrance of quite salt water into the Passage, presumably from the depths outside where *Calanus* was known to be abundant.

RAINFALL AND SHIFTING OF PLANKTON

On August 8 and 9, 1951, heavy rain (4·66 to 1·39 in.) fell over the drainage basin of the Digdeguash River. The course of the discharge from the River into the head of Passamaquoddy Bay was measured with a gauge at the first bridge above the point where the River falls into the tidal Digdeguash Basin (Fig. 3). The heaviest discharge was on August 10.

The progress of the outflow of fresher water was determined, beginning at different points on August 12, 13 and 14, by getting the salinities of surface samples taken daily at high water at four different points: (1) near the mouth of the Digdeguash estuary (James Carson's shore); (2) Indian Point at St. Andrews; (3) Mascabin Point in the outer part of Letite Passage; and (4) Wilson's Beach in the outer part of Head Harbour Passage. The results (Fig. 4) showed that the greatest effect at St. Andrews was on August 14, and that there was a clear effect at Wilson's Beach only on August 18. On that same day, the most marked effect appeared at Mascabin Point. But there was a complexity, which seems to have been owing to the facts that there is on the whole more inward than outward movement through Letite Passage, and that the outflow is largely through the main Head Harbour Passage. Along such course, Letite Passage and St. Andrews are on opposite shores of the half-way point. When the fresher water was most noticeable at St. Andrews four days after the heaviest discharge, there was very slight freshening at Mascabin Point in Letite Passage. But, another four days later, when the freshening was definite at Wilson's Beach, there was a more marked freshening at Mascabin Point. This is evidence that the outflow through Head Harbour Passage, which would be with the ebbing tide, was being carried with flooding tide north to the entrance into Letite Passage. At high tide, therefore, the latter showed a greater effect from this than did Head Harbour Passage itself. The slighter drop at Mascabin Point on August 17 indicates that the fresher water was issuing from Head Harbour Passage on that day. Entrance of fresher water into the Bay through Letite Passage on August 17 and 18 serves to explain the

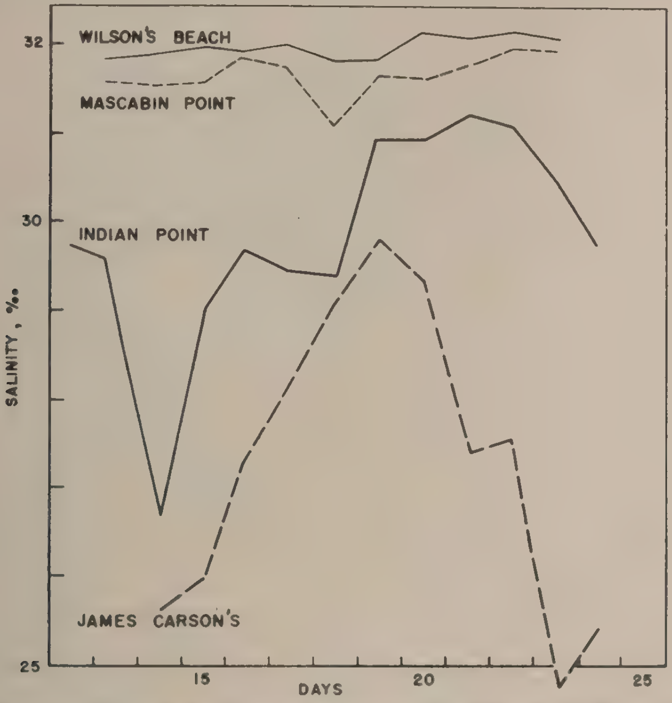

Fig. 4. Shore salinity at high water at four different points in Passamaquoddy Bay and in the related Passages on successive days in August, 1951, following freshets on August 10 and 19.

otherwise anomalous slight drop in salinity at St. Andrews on those days. This would mean that the fresher water was in part making a circuit around Deer Island in its position between the two Passages.

It will be noted in Fig. 4 that the crest of the fresh water flood was sharp and lasted about a day only, at St. Andrews, while at Wilson's Beach it lasted for two days and was little pronounced. The definite return of salter water to Head Harbour Passage was on August 20, that is, 11 days after the rainfall of August 9. This is in agreement with the data for the rainfall of September 17–18, 1933, which gave no increase in deep salinity at the inner end of Head Harbour Passage until 11 days or more later.

At the time of the freshet in 1951, August 9–10, *Calanus finmarchicus* was abundant in the passages leading out of Passamaquoddy Bay. There was also a most unusual plankton in the Bay, namely large numbers of Salps, mainly *Salpa fusiformis* and a few *S. zonaria*. *Salpa* seemed to be largely concentrated in the Bay, as *Calanus* certainly was in Head Harbour Passage. Such differential distribution was shown in tows made at 15 metres depth with a net of No. 5 mesh on August 8 at four stations, which were in the centre of the Bay (C_4), in the middle of Letite Passage (C_8), at the inner end (C_{24}) and at the outer end (C_{15}) of Head Harbour Passage. At these stations in the order given, the numbers of large *Calanus* and of *Salpa* respectively were as follows: C_4, 0 and 5; C_8, 28 and 0; C_{24}, 0 and 1; C_{15}, 347 and 1. The Salps must have come from the " Gulf Stream " water of the open Atlantic outside the continental slope, but they were, as near-surface forms, concentrated in the Bay, as was the locally produced *Aurelia*, which is quite in evidence in calm, clear weather. In contrast, *Calanus* was, as a deep-living form, concentrated in the Passages, as was also *Sagitta elegans*, another immigrant from the depths of the Gulf of Maine.

Surface tows were taken daily at Wilson's Beach in the outer part of Head Harbour Passage with net of No. 0 mesh from August 11 to 23. The numbers of *Calanus* in hundreds on successive days were: 347; 312; 712; 125; 372; 108; 34; 23; 6; 21; 104; 78; and 525. It will be noted that the number was definitely down by August 17 and lowest on August 19, with marked recovery by August 21. The numbers of *Sagitta*, although small, show a similar course: 9; 3; 18; 10; 14; 1; 2; 1; 0; 2; 2; 5; 17. The freshet seemed to exert an effect in removing *Calanus* and *Sagitta* from the Passage, beginning perhaps on August 16, reaching a peak on August 19, and passing away by August 23 with full return of these planktonts. The freshet would thus have worked out of the Bay through Head Harbour Passage during a period of six days, centred on the 10th day after the rainfall, or the 9th day after the peak of the discharge into the head of the Bay.

Euphausiid Crustaceans, of the genera *Meganyctiphanes* and *Thysanoessa*, are also indicative of deep indraught from the Gulf of Maine. Like *Calanus* and *Sagitta*, they were to be found in Head Harbour Passage at the time of the freshet. They occur in schools and more or less avoid the net, which made their numbers in the plankton hauls less representative of their distribution. The numbers of individuals of those two genera respectively in the hauls of successive days from August 11 to 23 were: 1 and 0; 0 and 0; 10 and 4; 1 and 1; 14 and 0; 4 and 0; 5 and 1; 0 and 0; 451 and 3; 29 and 110; 85 and 22; 15 and 4; and 24 and 0. There was thus a marked increase in their numbers on August 19, at the very beginning of the strong resurgence of salter water as shown at St. Andrews and at Mascabin Point, rather than at Wilson's Beach. It may be inferred that they had been in much greater abundance in deep water outside the Passage than in the Passage. The Amphipod Crustacean, *Euthemisto compressa*, another immigrant from the Gulf of Maine, was present in quite small numbers which for the successive days were: 0; 0; 3; 6; 2; 8; 1; 2; 7; 7; 22; 26; 17. Its numbers definitely increased on August 21.

Salpa fusiformis and *S. zonaria* were taken in the hauls on successive days in the following numbers respectively: 44 and 18; 28 and 0; 34 and 0; 71 and 1; 54 and 0; *214* and 0; *73* and 0; *22* and 0; 45 and 2; 23 and 1; 181 and 1; 25 and 2; 44 and 0. Since the more abundant species was in the aggregated stage, in which the individuals are attached together in rather long strings of as many as 18 individuals, there is considerable variation in its numbers, which will, therefore, not reflect very well its general abundance at the time and place. However, the numbers in italic mean that on August 16, 17 and 18 the individuals were in poor condition. It is to be expected that such open ocean forms as these would be injured by exposure to low salinity, and indeed those concentrated in the Bay were to be found in considerable numbers dead on the beaches as left by ebbing tide. It may be inferred that individuals that had been damaged by low salinity in the Bay were being carried out as the freshet worked out through the Passage. On this basis, the outflow occurred on August 16, 17 and 18, and the resurgence of salter water began on August 19. This agrees with the behaviour of the Euphausiids.

DISCUSSION

The passage of fresh water through Passamaquoddy Bay and Head Harbour Passage from the Digdeguash River to the Bay of Fundy may be expected to vary in time with the forces that effect it. One of these variable forces is the hydrodynamic effect of lighter water at the head of Passamaquoddy Bay than in the Bay of Fundy outside. This will vary with the amount of warm and fresh, and thus relatively light, water discharged by the Digdeguash River. The freshets of September 18, 1933, and of August 9, 1951, would provide a strong force to drive the water through the Bay and the Passage. Correlatively, the heavy outside water would be driven inwards. This force would operate at the outer end of the Passage only when the fresher water reached that far.

Following the 1933 freshet, the greater force set in motion was clearly acting in the Passage between 8 and 11 days after the rainfall, as shown after 11 days by high salinity at the inner end and a great abundance of *Calanus* in the outer part. Following the 1951 freshet, the fresher water was in the Passage 7 days after the rainfall, as shown by drop in abundance of *Calanus* and *Sagitta* and by appearance of many *Salpa* in poor condition. The greater force had clearly acted through the Passage by 10 days after the rainfall, as shown by *Salpa* in good condition, as well as by increased numbers of Euphausiids and *Euthemisto*. By that same time, there were sharp rises in surface salinity at Mascabin Point and at St. Andrews.

It would seem to have taken in 1951 9 days, with the main discharge one day after the main rainfall, for the peak of the freshet to pass from Digdeguash Basin to the outer part of Head Harbour Passage. What relation this has to the calculated average flushing time of about 15 days for the Bay alone is uncertain. The latter is based upon average conditions, and certainly not upon the conditions following a freshet, as the authors clearly state (KETCHUM and KEEN, 1953).

Whatever may be the complex conditions in Passamaquoddy Bay, it seems clear that a freshet, in working out through the heavily stirred Head Harbour Passage to the Bay of Fundy, at first carries plankton into the Passage from within and also out from the Passage. Then, with a reflux of outer water, it brings deep-water forms into the Passage from without. The latter is of particular importance for providing food for herring. The fattest herring of the whole region are those in this Passage and its associated waters, namely Harbour de Loutre and Cobscook Bay (Battle, *et al.*, 1936).

ACKNOWLEDGEMENTS

The Atlantic Biological Station provided facilities for this work both in 1933 and in 1951. In the latter year, Messrs. Raymond Doucette and James Carson, weir operators at the Digdeguash, Mr. Prescott Dines, lighthouse keeper at Letite, and Mr. E. M. Steeves, Fishery Officer at Wilson's Beach, gave assistance. Also, Mrs. E. Jermolajew counted the planktonts.

REFERENCES

Battle, H. I., Huntsman, A. G., Jeffers, A. M., Jeffers, G. W., Johnson, W. H. and McNairn, N. A. (1936), Fatness, digestion and food of Passamaquoddy young herring. *J. Biol. Bd., Canada*, **2** (4), 401–429.

Clarke, G. L. (1933), Diurnal migration of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. *Biol. Bull.*, **65** (3), 402–436.

Cushing, D. H. (1951), The vertical migration of planktonic Crustacea. *Biol. Rev.*, **26**, 158–192.

Esterly, C. O. (1919), Reactions of various planktonic animals with reference to their diurnal migrations. *Univ. Calif. Publ., Zool.*, **19** (1), 1–83.

Fish, C. J. (1936), The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.*, **70** (1), 118–141.

Hjort, Johan (1919), *Report of the Canadian Fisheries Expedition*, 1914–1915. *Dept. Naval Service, Canada, Sess. Pap.* 38*b*.

Huntsman, A. G. (1927), The Passamaquoddy Bay power project and its effect on the fisheries. *Telegraph-Journal*, Saint John., N.B. (also privately printed).

Huntsman, A. G. (1934), Herring and water movements. In: *James Johnstone Memorial Volume*, Univ. Liverpool Press, 81–96.

Ketchum, B. H. and Keen, D. J. (1953), The exchange of fresh and salt waters in the Bay of Fundy and Passamaquoddy Bay. *J. Fish. Res. Bd., Canada*, **10** (3), 97–124.

Russell, F. S. (1926), The vertical distribution of marine macroplankton. IV. The apparent importance of light intensity as a controlling factor in the behaviour of certain species in the Plymouth area. *J. Mar. Biol. Assoc., U.K.*, **14** (2), 415–440.

Wright, N.E. (1929), In: Report on the work of the Biological Board for 1928–29 (Cowie, J. J.). *Ann. Rept., Fish. Br., Dept. Mar. Fish., Canada*, **62**, 121–139.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 331-334.

Characteristics of surface water at Weather Ship J *

By R. B. Montgomery
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Summary—Surface temperature and salinity observed 15 times a month for 3 years at Weather Ship J, west of Ireland, are presented in two-dimensional frequency distribution on a temperature-salinity diagram.

The temperature-salinity diagram was introduced by Helland-Hansen (1916). Helland-Hansen and Nansen (1926) and others have used it as a scatter diagram for representing a large number of discrete, non-uniformly spaced observations. The purpose of the present paper is to demonstrate the suitability of the temperature-salinity diagram for quantitative representation of frequency distribution of water characteristics. A uniform series of data is used to prepare a diagram for a fixed point in the ocean.

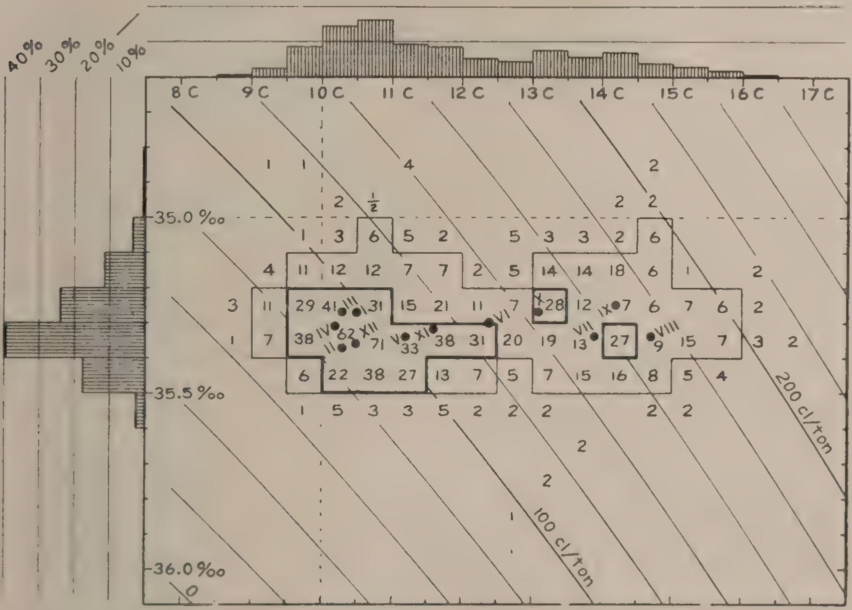

Fig. 1. Annual temperature-salinity diagram for surface water at Weather Ship J, 1948–1950. Number of occurrences per thousand is entered in each square (blank squares have no occurrence). Heavy frequency isopleth (21½ per mille) surrounds 51 per cent of occurrences, fine frequency isopleth (5½ per mille) surrounds 89 per cent. Monthly means are plotted as dots, each month identified by a Roman numeral. Anomaly of specific volume is shown by the family of curves.

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The weather ships, occupying nearly fixed positions, are potential sources of data of great climatological and oceanographic interest. Surface water at Weather Ship J in the North Atlantic Ocean is chosen for the present example, because published observations are available for three years in *Bulletin Hydrographique pour l'année* 1948, 1949, 1950. The data are credited to the Fisheries Laboratory, Lowestoft, Great Britain. Station J lies west of Ireland and south of Iceland. The usual position up to March 1950 was in the 1-degree quadrangle with southeast corner at 53° N 18° W and from April 1950 was in the quadrangle with southeast corner at 52° N 20° W.

For most days there is one observation of temperature and salinity, but for some days there is none. In order to obtain a homogeneous series from the somewhat irregular original series, 15 observations have been chosen for each of the 36 months. If available, the odd days 1, 3, . . . 29 have been used. Missing odd days have been replaced with other days or with observations from nearby positions. January 1948 has the fewest observations, only 10, and has been completed by including 4 from late December 1947 (*Bulletin Hydrographique pour l'année* 1947) and 1 from early February 1948.

The homogeneous series of 540 observations serves as the basis for the statistics presented on the temperature-salinity diagram in Fig. 1. The frequency for each two-dimensional class with temperature interval 0·5 C and salinity interval 0·1 per mille is tabulated in per mille.

By arranging the frequencies in order of decreasing magnitude and summing cumulatively, the result is found that about half (51 per cent) of the observations fall in classes with frequency 22 per mille and greater; these classes are enclosed by a heavy line. About nine tenths (89 per cent) fall in classes with frequency 6 per mille and greater; these are enclosed by a fine line.*

Summing the two-dimensional distribution horizontally and vertically respectively gives the one-dimensional frequency distributions of salinity and temperature, shown by the histograms at the left and top of Fig. 1.

Three-year monthly means for Weather Ship J are shown as points in Fig. 1. This method of showing monthly means was used by NEUMANN (1940, Abb. 25). His *Feld* 1 (Abb. 25, Nr. 6), the 5-degree quadrangle with northeast corner at 50° N 20° W, is represented by a circuit of similar shape (nearly isohaline), but with temperature range 1·5 C greater, mean temperature 2 C higher, and mean salinity 0·4 per mille higher.

Specific volume of surface water at Weather Ship J is shown by including isopleths of specific-volume anomaly. This quantity (which for surface water equals thermosteric anomaly) is chosen in preference to density or sigma-*t* for the reasons presented by MONTGOMERY and WOOSTER (1954). Any other temperature-salinity function, such as sound speed or surface concentration of dissolved oxygen, could be shown in the same manner by including the appropriate family of isopleths.

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* Two items of terminology are needed for two-dimensional frequency distributions. First, for a frequency isopleth of stated frequency a handier term than Bilham's "constant-frequency graph" (BROOKS and CARRUTHERS, 1953) is desirable. Secondly, an even more useful term would represent a frequency isopleth that encloses a stated proportion of the occurrences. If the first isopleth were called alpha and the second beta, the 0·0055-alpha would separate 5-per-mille classes from 6-per-mille classes, while the 0·9-beta would enclose nine-tenths of the occurrences; in Fig. 1, these two isopleths coincide. The betas have the advantage of being approximately independent of class intervals, for the alphas expand as the class intervals increase. It may be noted that beta is not similar to the term quantile (BROOKS and CARRUTHERS, 1953) used with regard to one-dimensional frequency distributions, because the maximum frequency coincides with 0-beta but with an intermediate quantile.

For lack of information, the accuracy of the observations is not discussed here.

The frequency distribution in Fig. 1 is self-evident, but some aspects are noteworthy. There is no apparent correlation between temperature and salinity at Weather Ship J. The frequency distribution of salinity is symmetric, but those of temperature and specific-volume anomaly are very asymmetric.

The peak frequency of temperature occurs near the minimum temperature. This pattern reflects the annual variation, which has a blunt minimum and a sharp maximum. Presumably the explanation is to be found, at least in part, in the deep, persistent winter mixed layer of large heat capacity in contrast with the shallow, changeable summer mixed layer.

The two-dimensional frequency distribution contains a suggestion of a waist at middle temperatures and of a secondary peak at higher temperatures. Whether these features will remain if the series is extended over more years is uncertain.

It seems likely that the pattern of annual frequency distribution of water temperature at Weather Ship J is characteristic of a large region in middle latitudes, but some very different patterns can be expected for other regions. As found by HESSELBERG (1943, p. 14), SIPLE (1949-1952), and FEUSSNER (1952, Abb. 4), the annual frequency distributions of air temperature at some land stations in middle latitudes show a rather symmetric bimodal pattern.

The annual frequency distribution of temperature is an economical expression of the temperature climate and might well be used more widely. The three references above are the only ones the author has found that employ this method.

The extreme range of temperature in the present series is 7·9 C,* while the difference in mean temperature between the warmest and coldest month is only 4·5 C. The frequency of temperatures below 10 C and above 15 C, hence outside the range of 0·5-C classes containing monthly means, is 17 per cent. It is clear that monthly mean temperatures, which are often the only statistics presented in climatological summaries, give but a faint picture of temperature conditions.

A welcome departure from the usual adherence to monthly means is offered by several series of oceanic Monthly Meteorological Charts published by the Meteorological Office, London. These charts include upper and lower 5-percentile isotherms of both air and water temperature, based on 2-degree quadrangles. The preparation of these charts must have entailed compiling further statistics that would be of interest if published.

The temperature-salinity diagram is but one of the oceanographic and meteorological class that has been called characteristic diagrams (MONTGOMERY, 1950), all of which would be suitable for the representation of frequency distributions.

Acknowledgements—The author wishes to record his benefit and pleasure from discussing this subject with Mr. JOHN D. COCHRANE, Mr. ARNOLD COURT, and Dr. JOHN B. LEIGHLY.

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* With access to all data, FRANKCOM (1954) reports the extremes at Station J as maximum 17·8 C and minimum 7·8 C.

REFERENCES

BROOKS, C. E. P. and CARRUTHERS, N. (1953), Handbook of statistical methods in meteorology. London, Her Majesty's Stationery Office, M.O. 538, 412 pp.

FEUSSNER, K. (1952), Über Wert und Verwendbarkeit von Temperatur-Häufigkeitsverteilungen für die Urteilsbildung. *Ber. Deutsch. Wetterdienstes, U.S. Zone*, **7,** (42), 440–446.

FRANKCOM, C. E. N. (1954), " Half-century " of voyages by each of the British ocean weather ships. *Meteor. Mag., London*, **83,** 282–283.

HELLAND-HANSEN, BJØRN (1916), Nogen hydrografiske metoder. *Forh. Skand. Naturf. Møte*, 357–359.

HELLAND-HANSEN, BJØRN, and NANSEN, FRIDTJOF (1926), The eastern North Atlantic. *Geofys. Publ.*, **4,** (2), 76 pp., 71 pls.

HESSELBERG, THEODOR (1943), Die Verwendung des Maxwellschen Verteilungsgesetzes auf meteorologische Häufigkeitskurven. *Geofys. Publ.*, **13,** (9), 19 pp.

MONTGOMERY, R. B. (1950), The Taylor diagram (temperature against vapor pressure) for air mixtures. *Arch. Meteorol., Geophys., u. Bioklim.*, (A), **2,** 163–183.

MONTGOMERY, R. B. and WOOSTER, W. S. (1954), Thermosteric anomaly and the analysis of serial oceanographic data. *Deep-Sea Res.*, **2,** 63–70.

NEUMANN, GERHARD (1940), Die ozeanographischen Verhältnisse an der Meeresoberfläche im Golfstromsektor nördlich und nordwestlich der Azoren (Aus den wissenschaftlichen Ergebnissen der internationalen Golfstrom-Unternehmung 1938, 1. Lief.). *Ann. Hydrogr. Mar. Meteorol.*, **68,** (Beiheft zum Juniheft), 87 pp.

SIPLE, P. A. (1949), American climates. *Bull. Amer. Inst. Archit.*, Sept., 16–36. (Also subsequent numbers.)

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Manganese nodules and oceanic radium

By Hans Pettersson
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The manganese nodules found by the *Challenger* Expedition in great depths have been studied by Sir John Murray and A. F. Renard (1891). They were recognized as products of a very slow growth, from manganese dioxide and ferric hydroxide, accumulated round a nucleus, a fragment of waterlogged pumice, or a shark's tooth or some other object lying on the surface of the deposit. Chemical analyses carried out by Brazier *et al.* proved a considerable number of trace elements like copper, cobalt, nickel, barium and lead to be present in the nodules. Of special interest was their relatively high content of radium first proved through measurements made by J. Joly (1908).

As I have been engaged on determinations of the radium present in deep-sea deposits since 1921 (1930; 1939; 1953), and later also of the radioactivity of sea-water, my interest was attracted by the radium contained in the nodules. The close affinity between radium and manganese,* well known from deposits at thermal sources on the continents, is no doubt responsible for the entry of radium into the manganese nodules. Granting this to be the case, I assumed that this radium is " unsupported " by its parent element ionium, in which case it should decay with age and consequently also with the depth below the surface of the nodule, according to the half-value period of radium, about 1,600 years.

Thanks to the courtesy of the British Museum of Natural History I obtained from their *Challenger* collections two small nodules, and through a similar courtesy of the Mineralogical Department of the Riksmuseum in Stockholm one half of a much larger nodule, also from the *Challenger* Expedition.

The results of my measurements on samples from these nodules, taken from thin layers in the surface and further inwards, confirmed my assumption. The radium content per gram of the samples fell off from a very high value in the uppermost surface, sometimes exceeding 100 units of the 12th decimal place, to a few units 7 to 10 mm deeper down. The rate of decline proved to be more rapid on the lower, flattened, side of the nodule, on which it had presumably been lying on the bottom, than on the upper, convex, side which must have been exposed to the settling of sediment from above, increasing the rate of growth over the value due only to aggregation into the nodule. The rate of radial growth, calculated from the decrease in radium, proved to be rather less than 1 mm in 1,000 years on the lower side and about 50% more on the upper, convex, side (1943).

The conclusion drawn from these measurements was, that the radium in the nodules is accumulated from the surrounding sediment. These results made it most desirable for me to obtain also other nodules from other parts of the ocean. Through the kind intervention of Dr. BIGELOW I obtained from the Harvard Museum of Comparative Zoology three manganese nodules, raised out of great depths in the SE Pacific Ocean, from Dr. AGASSIZ's expeditions with the *Albatross*.

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* An addition of small quantities of powdered " braunstein " and a thorough shaking of the mixture has been proved through experiments in Göteborg, to be a most efficient method for extracting radium and its isotope ThX from extremely dilute solutions.

Measurements of the radium content of these nodules were started in 1944, soon after they had arrived in Göteborg. However, due to pressure of other work in connection with preparations for a Deep-Sea Expedition with the Swedish *Albatross*, the values I found have not previously been published. As the results in some respects extend those of my earlier publication I have found the occasion propitious for publishing them here, expressing at the same time my sincere gratitude to Dr. BIGELOW for his generous help, not only in this connection but also in other matters, and for the most valuable discussions it has been my privilege to have with him.

NODULES FROM THE "ALBATROSS" PACIFIC CRUISES UNDER DR. AGASSIZ

The nodules obtained were from three stations visited during the Third Expedition. The following descriptions are quoted from J. MURRAY and G. V. LEE (1909, p. 144):

> *Station* 13. Lat. 09° 57′ N, long. 137° 47′ W, depth 2,690 fathoms. "At this station a large quantity of nodules was dredged, one of which is figured in Dr. ALEXANDER AGASSIZ's preliminary report. . . . They average 4 to 6 inches in diameter, and are all irregularly spherical or irregularly cubical, and never tend to form slabs. Their most conspicuous feature is the high degree of mammillated structure: the whole surface is covered with large protuberances, which may be as much as one inch in diameter. Sometimes these protuberances may be compounds, that is, formed of smaller ones, grafted the one on the other. On the one side of the nodule the mammillae have a relatively smooth surface, on which rubbing will develop a shining lustre; on the other side the mammillae are more dull, with a shagreen-like appearance."

Table I

Station Albatross 13. *Lat. N* 9° 57′. *Long. W* 137° 47′. *Depth* 4923 *m*

Average "depth"	*Radium in* 10^{-12} *g/g*	*MnO$_2$*	*Fe*
0·2 mm upper side	38	18·2%	13·3%
3·3 mm	5·4	29·3	13·2
11 mm	3·6	20·9	18·2
1·0 mm lower side	102		
3·5 mm	19·5		
5·8 mm	9		
13 mm	3·5		
0·15 mm upper side	61		
0·45 mm	33		
0·75 mm	26		
1·1 mm	34		
1·6 mm	16·7		
2·1 mm	7·2		
4·0 mm	8·2		
4·6 mm	10		
0·15 mm lower side	189		
0·2 mm	180		
0·6 mm	103		
1·0 mm	85		
1·5 mm	67		

As in earlier experiments, thin layers were removed from the surface and from layers immediately below it. Weighed quantities from these samples were dissolved in hot hydrochloric acid, leaving a small undissolved residue, which was practically free from radium. In some of the samples the content of manganese and of iron were measured by colorimetric methods. The first column in Table I gives the average " depth " of the sample below the surface of the nodule, the second column gives the content of radium in the usual units of the 12th decimal place in gram per gram of the sample. The maximum values obtained from the lower surface of the nodule are seen to be 102 and 189 units of Ra, respectively, whereas from the upper surface the values come out much lower, i.e. 38 and 61 units respectively. The fall-off in radium inwards is quite steep, to one half of the surface value or less for an increase in depth of 1 mm. Attempts to calculate the rate of radial growth from the rate of this fall-off gave values ranging from 0·6 mm to 1·4 mm in 1,000 years. The percentage of iron is fairly high, between 13 % and 18 %, whereas the content of manganese is of the same order varying between 18 % and 29 % of MnO_2.

Table II

Station Albatross 173. *Lat. S* 8° 55′. *Long. W* 146° 32′. *Depth* 4462 *m*

Average " depth "	*Radium in* 10^{-12} *g/g*	*MnO_2*	*Fe*
0·2 mm upper side	64	23·2%	14·9%
0·2 mm lower side	114	19·1%	15·8%
0·1 mm upper side	51	19·1%	15·8%
0·35 mm	31	20·8%	15·65%
1·35 mm	15	20·6%	50·8%
0·05 mm	35		
0·14 mm	28		
0·28 mm	25		
0·7 mm	15		
0·2 mm lower side	81		
0·5 mm	65		

Station 173. Lat. 18° 55′ S, long. 146° 32′ W, depth 2,440 fathoms. The description of the nodules from this station given by MURRAY and LEE (1909, p. 146) runs as follows:

" These nodules . . . constitute one of the most remarkable hauls of the cruise. At this station, where the deposit is Red Clay, immense numbers were dredged, varying in size from that of a small hazel-nut to potato-shaped nodules, three or four inches in diameter, and slabs over six inches in length. . . . Although the shape varies, the surface characters are absolutely constant, and belong to a type which was met with only at this particular spot. The surface of all the nodules, large and small, is *even*, that is to say, not covered with protuberances, but it is not *smooth*, being covered with numberless, closely set mammillae, giving it the appearance of shagreen or coarse leather. On account of the presence of these mammillae—1 mm in diameter, as a rule—the surface is dull, not shining. The colour is brown, never black. The external layer, from 1 to 2 mm in thickness, peels off easily. In some cases the layer coming next to it shows shagreen structure; in other cases it does not, being smooth. This external layer is generally the only one that can be removed: the rest of the nodule is very compact, and so hard as to be scratched with a knife only with difficulty. When whole and with no fracture previously existing, the nodules cannot be broken in the hand, even when great strength is exerted; the specific gravity is very high.

This nodule arrived in Göteborg broken into fragments. However, by piecing the fragments together it was easy to reconstruct the nodule and decide which had been its surface. The results from the measurements are set out in Table II, showing maximum values (presumably on the lower side)* of 114 and 81 units of Ra, whereas samples from the upper side contained much less radium, 64, 51 and 35 units respectively. The content of manganese was somewhat lower than in the nodule from Station 13, the content of iron being much the same except for one sample taken at a depth of 1·35 mm where an unusually high value of over 50% Fe was found. Two attempts to calculate the rate of radial growth from the fall-off in radium content gave a value of 0·4 mm in 1,000 years in each case.

The third nodule, taken from Station 4658, was the largest and, according to my view, the most remarkable of the three, both with regard to its shape and its colour. It is described by MURRAY and LEE (1909, p. 29):

> "The nodules from this station are as remarkable for their large size as for their constant shape, which is on a definite pattern. These nodules have each two surfaces, which are, roughly speaking, respectively dome-shaped and cone-shaped. Looking normally at one of the surfaces, the wider portion is circular, so that there is practically an axis of symmetry passing through the apex of both surfaces. The dome-shaped one is due to the aggregation of a few smoothly undulating bosses or protuberances of large radius. It is very smooth and black, with a metallic lustre, and has a distinctly scaly structure. The other surface is mammillated, has a dull colour and is incoherent, breaking up with little exertion of the fingers. A certain amount of clay is, moreover, mixed with the oxides, filling the cavities between the mammillae."
>
> "A section across a nodule shows it to be formed of successive concentric layers following exactly in their distribution the contours of the smooth surface. The innermost layer has absolutely the same shape as the outer one. The difference between the alternate layers is mainly one of hardness. In the samples cut, it has not been possible to find what was originally the centre of accretion; it probably consisted of some material which has since been transformed, or rather, replaced by the oxides.
>
> "This particular kind of nodule does not appear to have been described before; the nearest approach to it, as regards shape, is one represented in Fig. 4, Plate 3, of the '*Challenger* Report on Deep-Sea Deposits'" (MURRAY and LEE, 1909, p. 30).

A greater number of samples from this nodule than from the two others were submitted to analyses. Before sampling, the nodule was cut in two practically identical parts. The appearance of the section is shown in natural size by the drawing reproduced in Fig. 1, which reveals the concentric arrangement of the different layers in this cauliflower-shaped nodule. Its domed surface, presumably the upper one when lying on the sediment,† was smooth, whereas the lower, conical surface was scoriaceous, which made the sampling of this part rather difficult. Adopting MURRAY's views on the position of the nodule on the sediment surface, viz. that the scoriaceous, conical surface was the lower one, the higher radium values are ascribed to the lower surface with maxima varying between 85 and 330 units of Ra. The upper surface had much lower values, ranging from 25 to 61 units. The fall-off in the radium content with depth is more difficult to estimate, owing to the uneven, mamillated lower surface. With due reserve for this uncertainty we find the rate of radial growth in the downward direction comes out at only 0·15 mm in 1,000 years, which is only a fraction of the rate of growth in the upward direction, 0·4 mm in 1,000 years. The content of manganese in this nodule is seen to be very high, ranging from 30% to 75% of MnO_2.* On the other hand the content of iron is very low, averaging 1·3% of Fe, with an absolute minimum of only 0·03%.

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* According to a footnote given in the paper by MURRAY and LEE their views on the original position of this nodule differed (see above).

† Dr. LEE holds that the logical conclusion is that the cone-shaped mammillated surface is the upper surface, the smooth shining one being embedded in the clay, whereas Sir JOHN MURRAY takes the view, from his *Challenger* experience, that the smooth surface was the upper one, and points to Fig. 1, Plate IX, of the "*Challenger* report on deep-sea deposits" as confirmation of this, the smooth surface in his opinion being formed above the level of the deposit.

Low values of radium content were found in the nucleus and its vicinity, viz. 5 to 6 units of Ra. Still lower values were found in depths of from 4·5 to 15 mm in a series of samples taken from the back of the nodule, near the lower limit of the domed surface, where radium values as low as 2·2 to 2·4 units were measured. The results found with this extraordinary nodule, when summarized, seem to tell of an intense transfer of both manganese and radium from the sediment to the nodule, especially to the scoriaceous parts.

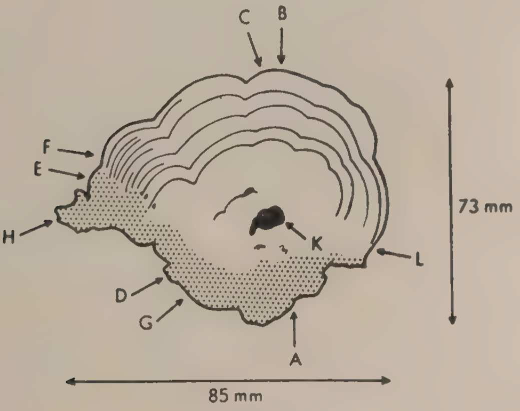

Fig. 1

It would have been most interesting to measure the radium, manganese and iron contained in the sediment surrounding this nodule, but unfortunately no sediment from the station was available. I collected instead a sample of the sediment entrapped within the nodule and measured it (last entry in Table III). The radium content was moderate (24 units), whereas the manganese dioxide was relatively low (9·1%), and the content of iron quite high for this nodule, viz. 4·1%. However, too much importance should not be attached to these figures, since an exchange between this entrapped sediment and the surrounding layers of the nodule may have occurred. With due reserve for the limited number of samples investigated, one may say that there is strong evidence for a transfer of radium from the sediment via the bottom water to the nodule, whereas the accretion of radium from the water column above is not likely to have occurred to a notable extent.

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* Only in one nodule, taken by the *Challenger* Expedition in the Pacific Ocean lat. 33° 31′ S, long. 74° 43′ W, depth 3,950, was a content of manganese dioxide as high as in this nodule reported by MURRAY and RENARD, viz. 77% MnO_2 in a nodule from blue mud. The iron content of that nodule was low, 4·5%.

By what kind of chemical action the solution of radium and other elements has taken place is unknown, owing to our ignorance regarding the chemical reactions, proceeding with immense slowness, in the contact region between sediment and bottom water.

Table III

Station Albatross 4658. *Lat.* 14° 29′. *Long. W* 81° 24′. *Depth* 4960 *m*

Series	*Average " depth "*			*Radium in* 10^{-12} *g/g*	*MnO₂*	*Fe*
a	0·3	mm	lower surf.	186	49·8%	3·2%
b	0·2	mm	upper surf.	58	43·4	6·0
b	3·2	mm	upper surf.	3·0	64·9	0·4
d	0·2	mm	Scoriacae	85	53·6	1·15
d	12	mm		29	58·3	1·3
e	0·2	mm	edge	46	68·2	0·95
f	0·2	mm	shell	31	71·2	1·0
c	0·5	mm	summit	25	66·7	1·7
c	0·5	mm	summit	9·5	68	1·1
c	2·5	mm		3·0	74·5	0·55
	0·5	mm	back of nodule	25	74·8	0·67
	1·5	mm		9·6	70·4	0·47
	2·5	mm		3·3	62·2	0·44
	3·5	mm		3·0	70·0	0·55
	10	mm		2·4	69·8	—
	15	mm		2·2	69·8	—
m	0·2	mm		61	—	—
m	0·5	mm		17·0	61·6	—
m	0·85	mm		10·0	61·4	—
k	14	mm	nucleus	5·5	64·9	—
k	14	mm	cavity	9·0	30·8	
g	0·15	mm	Scoriacae	160	44·7	1·0
g	0·7	mm	Scoriacae	13·7	64·4	0·03
g	1·3	mm	Scoriacae	3·0	62·1	0·14
h	0·2	mm	Scoriacae	330	44·5	0·35
			sediment	24	9·14	4·1
k	12	mm	nucleus	6·1	64·9	

It does not seem unlikely that submarine volcanic activity, which has undoubtedly played a dominant part in the building up of the islands and the "guyots" in the Pacific Ocean, may have given rise to magmatic acids, converting calcareous sediments into Red Clay and, at the same time, dissolved also other sediment components, thus facilitating their transfer into manganese nodules, manganese crusts and other concretions. It seems reasonable to assume that this acidulation has been concentrated to a relatively thin bottom layer over low-lying parts of the ocean floor.

OCEANIC RADIUM

The early hypotheses, put forward by JOLY and other early workers in the field, for the origin of deep-sea radium, have not withstood later criticism. This applies also to other explanations for the surprisingly high radium content in the deepest deposits.

(A) A precipitation of radium as insoluble sulphate from the water (JOLY).

(B) A production *in situ* from the uranium present in the sediment (JOLY).

(C) A cosmic origin of the radium, like that of the cosmic spherules (MURRAY).

(D) A magmatic origin from submarine volcanoes (MURRAY).

(E) A biological extraction from sea water by plankton organisms (EVANS, *et al.*, 1938).

Only the two last alternatives need to be considered seriously. The possibility that some of the deep sea radium is actually derived from volcanoes on the ocean floor cannot be denied. In several instances abnormally high radium values have been found both in the Tyrrhenian Sea and in the equatorial Atlantic, for which a magmatic origin seems probable. That radium to a certain extent becomes adsorbed by marine plankton has been supported by measurements in Göteborg and elsewhere. However, this biological extraction and subsequent transfer to the bottom deposits with siliceous or calcareous tests cannot be a *major* cause of the high radium content in deep-sea deposit. Such " unsupported " radium must have a highly transient existence in the very uppermost surface layer of the deposit.

In order to find a better explanation for the high radium content in the Red Clay and in the Radiolarian Ooze, found by JOLY and confirmed through my own measurements, teamwork on the radioactive elements present in ocean water was started by me over 20 years ago in Göteborg in collaboration with specialists from Vienna and Oslo (1939). By a special technique, extraction of radium from large-volume samples of sea water (20–40 litres), through co-precipitation with radium-free sulphate of barium, dependable values for the radium content were obtained. They turned out to be surprisingly low, in general less than one unit of the 13th decimal place. At the same time, accurate measurements of the content of uranium in sea water were, for the first time, carried out by means of a fluorescence method, developed by HERNEGGER and KARLIK (1935) of the Institut für Radiumforschung in Vienna. Their results indicated a fairly constant uranium content averaging $1{\cdot}3 \times 10^{-7}$ gr uranium per litre sea water of normal salinity ($35°/_{oo}$). In a state of radioactive equilibrium this uranium content would correspond to over $0{\cdot}4 \times 10^{-12}$ g Ra per litre of sea water, or to 6 times more than the radium actually found.

In order to explain this partial disappearance of radium from the sea water, I suggested in 1937 (1938), that its parent element, ionium, is being constantly removed from the water through a co-precipitation with ferric hydroxide, which is known to go on in the sea. This transfer of the ionium produced from dissolved uranium to the ocean bottom would explain the high radium content in deep-sea deposits as due to ionium-supported radium. From this ionium-precipitation hypothesis it would necessarily follow that the radium content in the deposit should increase to a near-surface maximum, attained about 9,000 years after precipitation, characterized by a radioactive equilibrium between ionium and radium. From there downwards in the sediment the content of the two elements should decrease together, according to the half-value period of ionium, about 82,000 years.

The first attempt to utilize the ionium-precipitation hypothesis for a submarine geochronology, based on radium measurements, was made in the early 70's by C. S. PIGGOT and W. D. URRY (1941) and by URRY (1949). Their first results, obtained from fairly long sediment cores from the Caribbean and the N. Atlantic Ocean (published as curves only), gave hopes of realizing a dependable method of dating different layers of a sediment core and of obtaining values for the rate of sedimentation from radium measurements. More extensive measurements on cores from the Swedish Deep-Sea Expedition, started after the return of the Expedition, are now being published by V. KRÖLL, who has for some years been working in Göteborg (1955). The results prove that the vertical distribution of radium in the cores is much more complicated than the ionium-precipitation hypothesis alone would imply. Often two, three, or even more maxima, beside that to be expected from radioactive equilibrium, Ra/Io, are actually found.

The opportunities offered by the Swedish Deep-Sea Expedition for studying the radioactivity of the ocean were used for an extensive sampling for radium analyses of large-volume water samples. After the return of the Expedition, the barium-sulphate precipitates were analyzed for radium, partly by the present author in Göteborg and partly in Vienna by Dr. TRAUDE BERNERT. The results, which have not been published before, are here set out in Table IV. They are seen to confirm our earlier results, viz. that the radium present in the ocean waters is only a small fraction of the quantity in equilibrium with dissolved uranium. In addition, uranium measurements on most of the water samples were carried out in Vienna by G. KOCZY (1950), with results agreeing with those found earlier by HERNEGGER and KARLIK. There cannot then be any doubt about the partial disappearance from the ocean waters of the radium produced from dissolved uranium.

However, a missing link in the chain of evidence concerns the presence of ionium in the deposits and in the water. Thanks to an ingenious method for photographic (nuclear-plate) determinations of ionium, Dr. E. PICCIOTTO and his co-workers in the Institut des Recherches Nucleaires of the Université Libre in Brussels, have been able to measure the ionium contained in sediments from the Swedish Deep-Sea Expedition (1954). It was found that, within the limits of experimental accuracy, the ionium present is in radioactive equilibrium with the radium in the same sample, except in the very uppermost surface layer, where there is an excess of ionium. On the other hand, more recent measurements of the ionium present in sea water, carried out by PICCIOTTO and F. KOCZY, have proved the ionium content to be extremely low, lower even than what could correspond to the radium content, which in itself, as we have seen, is only a fraction of the equilibrium value with dissolved uranium.

This result raises a problem of considerable interest. Since the scarcity of ionium in ocean water negatives the assumption that the radium in the water is produced *in situ* from its parent element ionium, the question arises, from what source is the radium contained in the ocean water derived?

Dr. F. KOCZY has proposed an explanation, put forward in a paper read before the meeting of the I.U.G.G. in Rome in Sept. 1954, that oceanic radium is dissolved through a chemical interaction between the bottom water and the uppermost 3–5 cm sediment layer. From the bottom water the radium is spread upwards through the water masses by diffusion, aided by turbulence. This view KOCZY finds supported by the curves in Fig. 3, giving the vertical distribution of the radium in the water column found from the measurements already quoted and set out in Table IV. The curves are seen to have maxima in the uppermost water layers, then to fall to intermediary minima at a depth of about 1,500 metres (possibly due to biologic extraction) and, after rising again to a maximum in a depth of 2,000 to 4,000 metres, attaining even higher values in still greater depths.

As has already been pointed out here on pp. 335 and 339, the passing over of radium from the sediment surface-layer to the manganese nodules resting on it speaks in favour of a solution of radium near or in the sediment surface actually taking place.

Accepting Dr. KOCZY's explanation as plausible, we arrive at a rather unexpected picture of the origin of the radium in ocean water.

The ancestral element uranium is being carried into the ocean by rivers from denuded rocks on the continents. The ionium produced from the dissolved uranium is very efficiently removed from solution through precipitation, and settles over the ocean bottom, there giving rise to its descendant radium. The radium in the uppermost few centimetres of the sediment passes readily over into solution, some of it becoming reprecipitated or adsorbed together with manganese in the nodules. Another part which has become dissolved from the sediment is distributed through the supernatant water masses, giving them a radium content intermediate between that in equilibrium with the dissolved uranium and the much lower quantity in equilibrium with dissolved ionium.

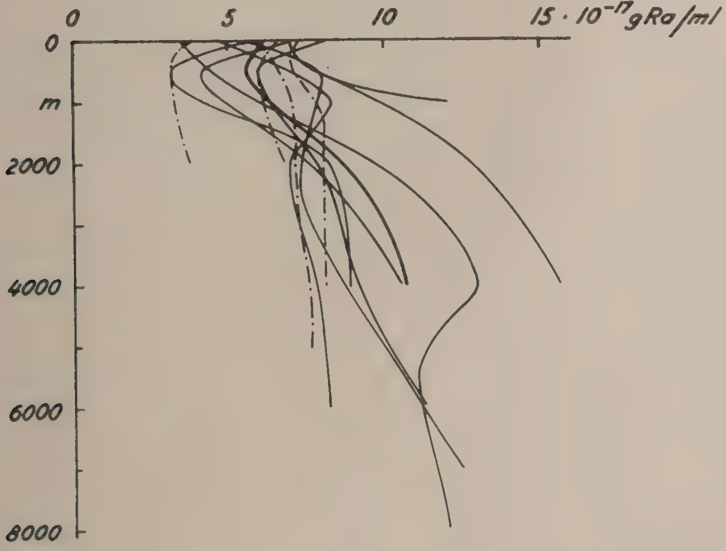

Fig. 3

Table IV

Lat.	*Long.*	*Depth*	*Ra g/Lit.* $\cdot 10^{12}$	*U g/Lit.* 10^{6}
N 00° 13′	W 18° 26′	25 m	0·07	1·1
		500 m	0·08	1·2
		2500 m	0·07	1·2
		5000 m	0·10	1·3
		7500 m	0·115	1·4
N 14° 15′	W 71° 02′	0 m	0·06	
N 14° 27′	W 66° 13′	1000 m	0·07	1·3
		3000 m	0·075	1·2
		5000 m	0·075	1·2
N 28° 05′	W 60° 49′	25 m	0·045	1·15
		500 m	0·07	1·2
		1000 m	0·08	1·4
		2000 m	0·07	1·3
		4000 m	0·08	1·3
		6000 m	0·08	1·1
N 43° 04′	W 19° 40′	25 m	0·05	
		500 m	0·06	
		1000 m	0·065	
		2000 m	0·065	
		4000 m	0·08	
		6000 m	0·11	
N 21° 24′	W 46° 24′	0 m	0·035	
		100 m	0·035	
		400 m	0·035	
S 02° 52′	W 89° 56′	20 m	0·09	1·1
		500 m	0·09	1·1
		1000 m	0·15	1·3
S 13° 24′	W 149° 30′	0 m	0·10	1·1
		1000 m	0·12	1·4
		2000 m	0·13	1·3
		3000 m	0·17	1·1
		4000 m	0·17	1·1
N 05° 10′	E 127° 53′	0 m	0·035	
		500 m	0·050	
		2000 m	0·10	
		4000 m	0·13	
		5700 m	0·11	
		8200 m	0·12	
S 01° 09′	E 126° 22′	3000 m	0·07	
S 00° 00′	E 88° 18′	10 m	0·055	
		500 m	0·05	
		2000 m	0·07	
		4000 m	0·09	1·3
N 10° 06′	E 52° 15′	20 m	0·05	
		500 m	0·04	
		2000 m	0·08	
		3750 m	0·11	
N 21° 09′	E 38° 07′	20 m	0·05	1·1
		500 m	0·06	1·3
		2000 m	0·06	1·1
N 35° 41′	E 21° 50′	50 m	0·065	
		1000 m	0·11	
		2000 m	0·07	
		4000 m	0·09	

Average: 0·078

REFERENCES

Evand, R. D., Kip, A. F. and Moberg, E. G. (1938), The radium and radon content of Pacific Ocean water, life and sediments. *Amer. J. Sci.*, (5), **36**, 241–259.

Föyn, Ernst, Karlik, Berta, Pettersson, Hans and Rona, Elisabeth (1939), Radioactivity of sea water. *Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handl.*, Femte Följden, (B), **6** (12), 1–44. (*Medd. Ocean. Inst., Göteborg*, No. 2.)

Hernegger, F. and Karlik, Berta (1935), Uranium in sea water. *Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handl.*, Femte Följden, (B), **4** (12), 1–15. (*Medd. Göteborgs Högskolas Ocean. Inst.*, No. 12.)

Isaac, N. and Picciotto, E. (1953), Ionium determination in deep-sea sediments. *Nature*, **171** (4356), 742–743.

Joly, J. (1908), On the radium content of deep-sea sediments. *Phil. Mag.* (6), **16**, 190–197.

Koczy, Gerda (1950), Weitere Uranbestimmungen an Meerwasserproben. *Osterreichische Akad. Wissenschaften, Sitzungsber. Mathem.-Naturw.* Kl., Abt. IIa, **158** (1–5), 113–121.

Kröll, V. S. (1955), The distribution of radium in deep sea cores. *Repts. Swedish Deep-Sea Exped.*, 1947–48, 10, (1), (in press).

Murray, John and Lee, G. V. (1909), The depth and marine deposits of the Pacific. *Mem. Mus. Comp. Zool., Harvard Coll.*, **38**, 1–169.

Murray, John and Renard, A. F. (1891), Report on deep-sea deposits. Chemical products formed *in situ* on the floor of the ocean. *Challenger Repts.*, 335–412.

Pettersson, Hans (1930), Teneur en radium des dépôts de mer profonde. *Rés. Camp. Sci., Monaco*, **80**, 1–50.

Pettersson, Hans (1938), Das Verhältniss Thorium zu Uran in den Gesteinen und im Meer. *Mitt. Inst. Radiumforschung*, 400a, 1.

Picciotto, E. and Wilgain, E. (1954), Thorium determination in deep-sea sediments. *Nature*, **173** (4405), 632–633.

Piggot, C. S. and Urry, W. D. (1941), Radioactivity of ocean sediments. III. Radioactive relations in ocean water and bottom sediment. *Amer. J. Sci.*, **239**, 81–91.

Urry, W. D. (1949), Radioactivity of ocean sediments. VI. Concentrations of the radioelements in marine sediments of the southern hemisphere. *Amer. J. Sci.*, **247**, 257–275.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 346-357.

The accumulation of river water over the continental shelf between Cape Cod and Chesapeake Bay *

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Summary—The depth mean salinities for the waters of the continental shelf between Cape Cod and Chesapeake Bay show a seasonal variation in the concentration of river water. The spring and the winter accumulations are about the same, but about 25% more river water is present in the summer. The total volume of fresh water in spring and winter is equivalent to that produced by the rivers in about one and a half years. The extra accumulation in summer is equal to half a year's flow, and reflects, in part, the fact that the high spring flows of two successive years are present on the shelf at this time.

There is a decrease in the average content of river water in the direction of the flow of the coastal current, in spite of the addition of river water along its course. It is concluded that considerable transport of river water and of salt normal to the coast is necessary. The horizontal mixing coefficients normal to the coast are computed from the seasonal changes in salinity. They range from 0·58 to 4·96 × 10⁶ cm²/sec, with the values for the decrease in salinity from spring to summer being smaller than those for the increase from summer to winter conditions. At both times, the values decrease with increasing depth and distance from shore.

PROFESSOR H. B. BIGELOW initiated extensive studies of the distribution of temperature and salinity over the continental shelf between Cape Cod and Chesapeake Bay in 1913. In a series of papers, he and his associates have described the seasonal variations and correlated these with vernal warming, river runoff and the water circulation of the area.

The sea water of this section of the continental shelf is greatly diluted by the fresh water continuously supplied by several major rivers. Both regional and seasonal variations in salinity are great, and the area is one of complicated dynamic structure and circulation. The accumulation of river water affords a direct means of evaluating the rate of the circulation and mixing when compared to the rate of discharge of the rivers. This approach has been used extensively in estuaries in recent years. While it may be unorthodox to treat this open coastal area as an estuary, it was felt that some of the methods of study should be informative, and provide a time scale for the circulation in various parts of the region.

The area included in this study (Fig. 1) extends across the continental shelf and slope from the coastline to the 1000 fathom depth contour. It is bounded to the north-east by a section extending SSE from the western tip of Martha's Vineyard, and to the south by a section extending ESE from the mouth of Chesapeake Bay. This region has a surface area of 104×10^{10} ft², or 29,000 square nautical miles, and contains a volume of water equal to 732×10^{12} ft³ or 3400 cubic nautical miles (Table I).

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The major rivers discharging into this region, their gaged drainage basin and the average rates of flow, are listed in Table II. The total drainage area is estimated to be 116,000 square statute miles, nearly 62% of which is gaged in these rivers. Assuming the ungaged area to have similar drainage characteristics, the total river flow into this region is 167,764 cubic feet per second. The volume of water contributed by the rivers annually is thus 5·29 × 10^{12} cubic feet, less than one per cent of the total

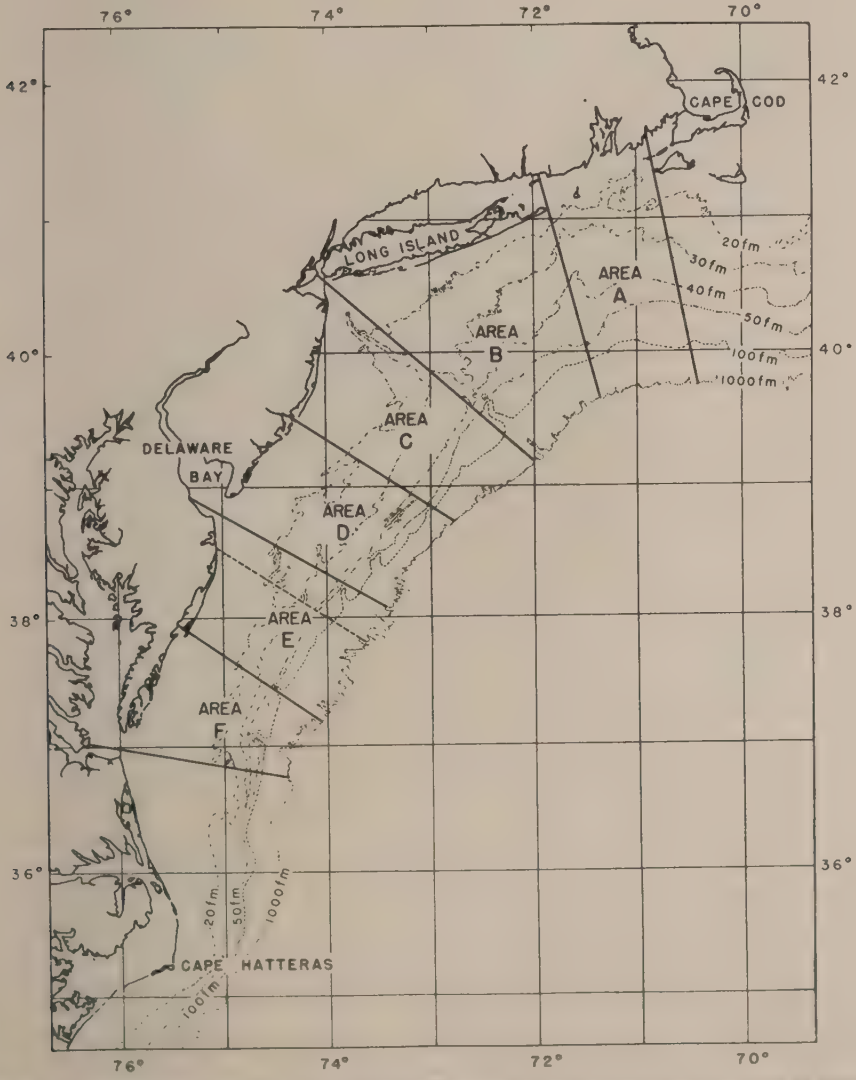
76°
74°
72°
70°
42°
40°
38°
36°
CAPE COD
LONG ISLAND
AREA A
AREA B
AREA C
AREA D
AREA E
AREA F
DELAWARE BAY
20fm
30fm
40fm
50fm
100fm
1000fm
CAPE HATTERAS

Fig. 1. The continental shelf from Cape Cod to Chesapeake Bay, showing the areas used in Table I and Fig. 2. The dashed line in Area E indicates the southern limit of Area D′ and the northern limit of Area E′ used for the summer observations.

volume of water within the region considered. The discharge of all of these rivers is already mixed with large volumes of sea water in the sounds and estuaries before reaching the continental shelf.

Table I

The total volume of water contained between depth contours for various areas of the continental shelf, Cape Cod to Chesapeake Bay

Depth range fathoms	Total volume (10^{10} ft³) within region						*Total*
	A	*B*	*C*	*D*	*E*	*F*	
0– 20	114	376	513	403	412	498	2316
20– 30	363	981	509	613	360	220	3046
30– 40	869	964	715	407	378	98	3431
40– 50	643	740	292	248	103	157	2183
50– 100	1170	954	648	423	621	205	4021
100–1000	8244	10386	8000	7151	17433	7038	58252
Total	11403	14401	10677	9245	19307	8216	73249

Table II

The major gaged rivers discharging between Cape Cod and Chesapeake Bay Data from U.S. Geological Survey Water-Supply Paper 1051

Group	*River*	*Years of record*	*Drainage area sq. miles*	*River flow ft³/sec.*	*ft³/sec/sq. mi.*
A	Thames	29	711	1210	1·70
	Connecticut	19	9661	16260	1·68
	Housatonic	19	1545	2494	1·61
	others*	—	1171	1702	1·45
C	Hudson	—	8090	16510	2·04
	Passaic	49	785	1442	1·83
	Raritan	—	779	643	1·31
D	Delaware	34	6780	11770	1·74
	Schuylkill	24	1893	2715	1·43
F	Susquehanna	16	25990	35650	1·37
	Potomac	17	11560	10830	0·94
	Rappahannock	40	1599	1648	1·03
	York	—	1072	729	0·68
	Total gaged:		71636	103603	1·45

* The Taunton, Providence, Pawtuxet and Pawcetuck Rivers gaged flow for 1946–1947.

Direct precipitation on the area would add $2{\cdot}38 \times 10^{12}$ ft³ per year, but the loss from evaporation would be $3{\cdot}42 \times 10^{12}$ ft³ per year. WÜST's data for 35° and 40° North Latitude of the Atlantic Ocean (SVERDRUP *et al.*, 1942, Table 30) give a mean precipitation of 2·29 feet and a mean evaporation of 3·29 feet per year. The excess of evaporation over precipitation of one foot per year gives a net loss for the exchanges across the sea surface of $1{\cdot}04 \times 10^{12}$ cubic feet per year. This is equivalent to 20% of the water supplied by river drainage. The remaining 80% must be transported through the region by advection and eddy diffusion, and mixed away in the more saline water offshore.

The Gulf Stream flows offshore, separated from the waters of the continental shelf by the slope water of intermediate characteristics (ISELIN, 1936, 1940). The upper 200 metres or so of the slope water is generally less saline than corresponding waters of the Gulf Stream, reflecting the effects of varying amounts of coastal water at different times of the year. Ultimately the river water which is not evaporated locally must be entrained, via the slope water, in the Gulf Stream system. The volume transport of the Gulf Stream varies between 76 and 93 million cubic metres per second (ISELIN, 1940). This flow is twenty thousand times greater than the rate of addition of river water to this part of the continental shelf, so that direct assimilation of all of this river water in the Gulf Stream would not make a measurable change in its salinity.

The general westerly and southerly drift of the inshore water is well known, and is indicated by the temperature and salinity sections given by BIGELOW (1933) and BIGELOW and SEARS (1935). Extensive current measurements from lightships throughout the area south of New York show non-tidal drifts largely paralleling the coast of from 1·8 to 2·8 nautical miles per day (ZESKIND and LELACHEUR, 1926; HAIGHT, 1938; MARMER, 1935). The non-tidal current observed at Ambrose Lightship flows nearly east, and little or no residual drift was observed at Nantucket Shoals Lightship except for transitory effects of the winds. *The Current Atlas of the North Atlantic Ocean* (Hydrographic Office, 1946) gives consistent westerly and southerly drifts, paralleling the coast for the inshore areas south of New York, with frequent easterly components over the mid shelf area south of Martha's Vineyard and east of both the Delaware and Chesapeake Bays.

The general character of these coastal drifts has been recently confirmed by drift bottle studies (REDFIELD and WALFORD, 1951; MILLER, 1952). Practically all of the bottles released close to shore south of New York drifted southward. Only two bottles, of several thousand released north of Cape Hatteras, were recovered south of that point, indicating an abrupt reversal of the current. Many of the bottles released to the east of New York were recovered north of the point of release, along the Long Island shore. The percentage returns of bottles released close to the coast was high, but decreased rapidly with increasing distance from the coast. Few bottles released more than 20 miles offshore were recovered on the beach, though several of these have crossed the Atlantic and have been recovered on European shores.

The question arises whether these drifts can be expected to add substantial amounts of fresh water to this area of the continental shelf. To the south, the Gulf Stream is very close inshore and the shelf is only 30 miles wide at Cape Hatteras. BIGELOW and SEARS (1935, p. 87) state: " Just south of Cape Hatteras a wedge of pure oceanic water presses in across the shelf entirely separating the shelf and slope water bands to the north from the low coastal salinities farther south ". All of the evidence thus indicates that no significant increment of fresh water may be expected to enter the area from the south.

The possibility that freshened Gulf of Maine water may enter the area through the Martha's Vineyard section cannot be categorically excluded. BIGELOW (1915) concluded that northern water in this area was hardly appreciable, except perhaps in unusual years. *The Current Atlas of the North Atlantic Ocean* shows southerly or easterly drifts most of the year south of Martha's Vineyard, and, when westerly components are present, adjacent currents suggest an eddy which does not penetrate beyond the tip of Long Island. Some of the drift bottles released by BIGELOW (1927) in the Gulf of Maine were recovered on Nantucket and Martha's Vineyard, but rarely entered the area under consideration. Several bottles, however, which were released in July 1922 outside the 50 fathom contour southeast of Cape Cod, were recovered along the coast to the west. A series of drift bottles were released in October 1951 from the *Caryn* between Cape Cod and Nantucket Lightship, but none of these were returned from within the area considered here. It is concluded that, although there may be some influx of fresh water from the northeast into the area, it cannot be evaluated, and is probably small relative to the volumes supplied directly by the rivers.

The details of the salinity distribution are given by BIGELOW and SEARS (1935). The following brief review of their conclusions will be helpful in understanding the general patterns. " The basic feature in the pattern of salinity of the region, the year around, is that isohalines tend to parallel the coastal trend with values increasing continuously from the shore, seaward, along any given profile normal to the coast" (p. 6). The salinity is at a maximum during the winter months when water of salinity lower than $32^{\circ}/_{\circ\circ}$ is found only in the mouths of Delaware and Chesapeake Bays. About 50% of the total annual discharge of river water is concentrated in March, April and May. This produces local and irregular freshening off the mouths of the rivers. The salinity off the Husdon River and Chesapeake Bay falls to $27^{\circ}/_{\circ\circ}$ 8–10 miles from land, and all of the inshore water is freshened to $32^{\circ}/_{\circ\circ}$ or less at this time. This vernal freshening may not culminate before late summer in exceptional years, though in all years of record the extent of water freshened to less than $32^{\circ}/_{\circ\circ}$ was greatest during the summer. The vertical stratification was also a maximum at this time, being most pronounced off Chesapeake Bay, and least over Nantucket Shoals to the northeast, where turbulence keeps the waters nearly homogeneous throughout the summer. During the autumn the vertical gradients of salinity decrease and the surface salinities increase, so that by January the distribution has returned to the winter maximum condition.

THE ACCUMULATION OF RIVER WATER

The total volume of river water accumulated in the area has been computed from the distribution of salinity. When this is compared to the rate of river flow, the average flushing time can be determined. The calculations have been made for three periods of the year, namely (1) April, May and June; (2) July, August and September; (3) October through March inclusive.

The fraction of fresh water (f) in any sample is given by: $f = \frac{\sigma - s}{\sigma}$

in which s is the salinity of the sample considered and σ is the salinity of the undiluted sea water. For this value we have taken $35^{\circ}/_{\circ\circ}$, since water of this salinity is found at the bottom along the continental slope, usually in a continuous band throughout this region. Data from 856 hydrographic stations were utilized. These included stations reported by BIGELOW and his associates, stations along the continental slope (ISELIN, 1936), and in the New York Bight (KETCHUM, REDFIELD and AYERS, 1951), as well as several stations occupied by the *Atlantis* and by other vessels of the Woods Hole Oceanographic Institution during recent years.

The volume of water between depth contour lines for the various areas shown in Fig. 1 are listed in Table I. These were computed from the planimetered surface area and the average depth which was obtained from the U.S. Coast and Geodetic Survey Navigation Chart ♯1000. All volumes, and the average fraction and accumulation of fresh water, are computed for the entire depth of the water column, the contour lines being the inshore and offshore limits of the area considered.

The average fraction of fresh water was computed from the graded depth mean of the salinity values for each station. The bottom bottle of each cast was used to characterize the water from that depth to the recorded or chart depth of the station. This results in an underestimate of the deep salinities, but the volume of river water calculated for the depths below the bottom bottle rarely exceeded 10% of the total river water, even for the summer observations when stratification was greatest and the error would be most pronounced.

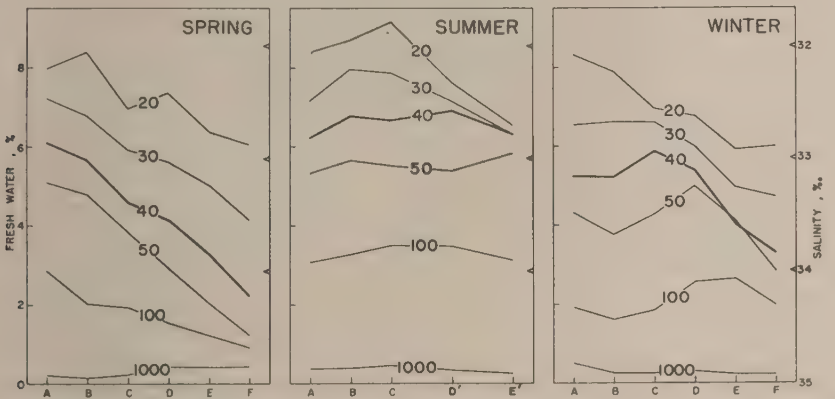

Fig. 2. The depth mean salinity and proportion of fresh water for various areas indicated in Fig. 1. The numbers on each line indicate the depth, in fathoms, of the outer boundary of the subdivision considered.

Spring: 328 stations occupied during April, May and June;
Summer: 203 stations occupied during July, August and September;
Winter: 325 stations occupied during October–March inc.

The average fraction of fresh water and the corresponding salinity for each sub-area of Fig. 1 are given in Fig. 2 for the three periods of year. The river water found in the spring period decreases from a mean value of 7·02% for the innermost portion (shore—20 fathoms) to a mean value of 0·33% over the continental slope (100–1000 fathoms). The values also decrease from north to south. This would not appear obviously from the salinity charts of Bigelow and Sears (1935) which show lower surface salinities to the south. However, they also show maximum vertical gradients of salinity in this area, and the average salinity over the entire water column is greater. The decreasing fresh water fraction to the south is observed for all of the depth ranges to the 100 fathom contour. Between the 100 and 1000 fathom contours the fresh water fraction decreases somewhat toward the north.

In the summer period the fresh water content is at a maximum for all fo the depth ranges, decreasing from 7·86% for the innermost band to 0·41% for the waters over the continental slope. Within the 30 fathom contour, there is an increase of fresh water content from the Martha's Vineyard section to the offing of the Hudson River, but to the southward there is a gradual decrease. Beyond the 40 fathom contour the fraction of fresh water shows little variation from north to south for the various areas.

The conditions observed in the October-March period have marked similarities to the spring distribution. The inshore band is least fresh (6·75%) at this time of year. There is, however, a considerable accumulation of fresh water from the middle of the shelf to the 100 fathom contour over the southern part of the area. All of the areas south of New York between the 30 and the 100 fathom contour contain greater proportions of fresh water than are found in these areas in the spring, though they are consistently less than the concentration found in these areas in the summer.

The decrease in the concentration of fresh water over the inner part of the shelf to the south is remarkable. As mentioned above, there is a consistent southward drift of the inshore waters, at least below New York, and there are substantial increments of fresh water from the Hudson, Delaware and Chesapeake Bay systems. Thus in each succeeding area some of the river water entering from the adjacent area, and the water locally added, must be dispersed across the shelf, and mixed locally with higher salinity water to give the observed decreases in average concentration. Although the 20 and 30 fathom contours are further off shore in the south, the volume available for dilution (Table I) is not enough greater to give the observed decrease in the concentration of fresh water. Qualitatively, such a distribution can be maintained only when the transport of fresh water normal to the coastline exceeds the transport parallel to the coast. This will be discussed further in the section on diffusion coefficients.

THE FLUSHING TIME

The ratio between the volume of river water accumulated and the rate of river flow gives the flushing time for the region. This has been calculated for the various depth ranges at three times of year with the result shown in Table III. The accumulation of river water during the spring (April–June) agrees closely with the accumulation found in the winter period (Oct.–March) and corresponds to the contribution from the rivers during a period of about one and a half years (1·61–1·65). The accumulation during the summer period (July–September) is about 25% greater than at the other times. Using the annual average river flow, this corresponds to nearly half a year of excess. This excess does not necessarily indicate a slower circulation at this time, but may reflect the excess river flow during the period of maximum discharge. The lag of 3–4 months before this excess discharge is recognizable over the shelf is not unreasonable for the time required for the exchanges through the estuaries and sounds. With a three-month lag period, this 25% excess accumulation during the summer corresponds to expectation since " fifty per cent of the total annual discharge of river water is concentrated in March, April and May " (Bigelow and Sears, 1935, p. 88) and since the excess spring flows of two successive years are represented by the accumulation during the summer. The surface inshore waters reflect this increased flow within a month after maximum river discharge, but on the average the maximum effect over the entire shelf is delayed, as would be expected considering the length of time required for transport of river water through the area.

Table III

Flushing times of the continental shelf between Cape Cod and Chesapeake Bay for an average river flow of $14{\cdot}5 \times 10^9$ *ft³/day* (167,764 *ft³/sec.*)

Depth Range Fathoms	*FLUSHING TIME, DAYS*		
	April–June	*July–Sept.*	*Oct.–March*
0– 20	112	125	108
20– 30	127	156	130
30– 40	119	157	123
40– 50	62	83	62
50– 100	52	91	56
100–1000	131	140	110
Total, days:	603	752	589

THE FLUX OF FRESH AND SALT WATER

The total transport through any complete cross-section must result in the movement seaward of a quantity of river water equivalent to the quantity contributed by the rivers in unit time if the distribution is to remain in steady-state. The cross-sections must completely surround the source of fresh water. Those we have used extend from shore at the eastern boundary of area A, to a depth contour, along the contour line to the southern boundary of area F, and back to the shore.

For any given part of the cross-section this transport is a complicated sum of the effects of horizontal and vertical advection and eddy diffusion. However, our method of averaging gives the depth mean salinity and obscures the vertical effects. Thus, it seems possible to treat the system as STOMMEL (1953) has treated estuarine circulation, as a two dimensional one in which the advection produced by river water entering the system is balanced by horizontal eddy diffusion normal to the coast.

The flux of material in the direction normal to the coast (F_x) is given by STOMMEL (1953):

$$F_x = Qc - SA\frac{dc}{dx}$$

in which c is the fraction of fresh (or salt) water, Q is the rate of river flow, S the cross-sectional area, A the horizontal mixing coefficient, and x is the distance normal to the coast. Under steady-state conditions the flux of river water through any cross-section equals the rate of river flow ($F = Q$), and the flux of salt through any cross-section is zero.

The eddy diffusion parallel to the coast has been neglected in the above equation. If the coefficient of horizontal diffusion is the same in the two directions, the transport by diffusion parallel to the coast must be proportionately very small. The gradients in this direction range from one tenth to one thirtieth the value of the gradients normal to the coast; and the cross-sectional areas at the ends are also small compared to the area along the contour line. For example, the product $S_x \triangle f / \triangle x$ is

400 times as great as the product $S_v \triangle f / \triangle y$ for the winter distribution and the 30 fathom contour. This product for the direction parallel to the coast never exceeds one per cent of the value normal to the coast.

As has been shown above, there is a decrease of salinity for this area between the spring and summer conditions, and a corresponding increase between the summer and winter conditions, with little or no change between the winter and spring conditions. Since the flushing time of the area is a year and a half, and these changes occur in shorter periods, the distribution cannot be treated as a steady-state. However, it is possible to evaluate the flux of salt from the seasonal changes, and to compute average mixing coefficients from these data. The necessary data are presented in Table IV, and the coefficients are given in Table V.

Table IV

The mean salinities at three seasons of year, and the flux of salt across different depth boundaries on the continental shelf between Cape Cod and Chesapeake Bay. The contours selected average 28 kilometers apart

Depth Contour Fathoms	*Mean Salinities ‰*			*Flux of Salt $10^7 g/sec.$*	
	Spring	*Summer*	*Winter*	*Sp.–Su.*	*Su.–Wint.*
20	32·54	32·24	32·64	2·53	— 2·24
30	32·88	32·40	32·84	7·86	— 5·48
40	33·24	32·69	33·18	14·68	— 9·52
100	34·06	33·57	34·04	25·78	—16·58
1000	34·88	34·86	34·91	30·03	—23·63

Table V

The coefficients of horizontal diffusion computed from the changes in salinity at different seasons of the year

Depth Contour Fathoms	*Horizontal Diffusion Coefficients $10^6 cm^2/sec.$*	
	Sp.–Su.	*Su.–Wint.*
30	2·52	4·96
40	1·72	3·41
100	0·58	1·48

The net flux of salt is positive for the change from spring to summer, since salt is being transported offshore in the plus x direction, and negative for the change from summer to winter when the salinity increases again. The net flux of salt resulting from changes from season to season range from about 15 to 50% of the offshore advection of salt with the river water escaping from the area. The coefficients of eddy diffusion (Table V) obtained for the spring-summer change range from 0·58 to 2·52 $\times$ $10^6 cm^2/sec.$, and the values obtained for the summer-winter change vary from 1·48 to 4·96 $\times$ 10^6 cm²/sec. At both times the value decreases with increasing depth and distance from shore. Although the vertical component of turbulence has been averaged out of the data, it is worth noting that the smaller coefficients are found at the time of year when vertical stability is developing to maximum values.

The value of horizontal mixing coefficients obtained for this area are in substantial agreement with previous determinations for coastal areas. SVERDRUP and FLEMING (1941) obtained a coefficient for the California coastal region of $2 \times 10^6 \text{cm}^2/\text{sec.}$; and BOWDEN (1950) computed coefficients for the Irish Sea ranging from 0·36 to $9{\cdot}0 \times 10^6 \text{cm}^2/\text{sec.}$

It has been mentioned above that inclusion of the excess spring river flow of two successive years could account for the excess accumulation of river water during the summer. Such an increase in river flow would increase the spring-summer coefficients of eddy diffusion by only about 25%, and would not make them as great as those observed for the summer-winter change. It must be concluded, therefore, that the excess accumulation of river water in the summer is a joint effect of the increased river flow and the decreased turbulence.

DISCUSSION

The flushing times estimated from the accumulation of fresh water, and some general aspects of the circulation, are approximately confirmed by the drift bottle studies described by MILLER (1952). Practically all of the bottles were recovered south of the point of release, confirming the net drift southward parallel to the coast. The proportion of returns decreased greatly with distance from shore, however, and very few bottles released more than 15–20 miles from shore were returned. This confirms, for the surface waters at least, the active offshore transport as well as the narrow band of current parallel to the coast.

The rate of drift of the bottles released near shore varied over wide limits. Several gave velocities greater than 10 miles per day, but all of these were released either just south of Delaware Bay or off Chesapeake Bay, where the net drifts appear to occupy a very narrow coastal strip. Most of the bottles drifted at rates of 3–5 miles per day. A bottle travelling at this rate, which did not beach en route, could traverse the 350 mile stretch of coast in 70–117 days. This corresponds approximately to our flushing time within the 20 fathom contour of 108–125 days. Since very few bottles were recovered from greater distances offshore, it is impossible to check our flushing times for the deeper areas in this way.

The flushing times are based upon the assumption that no substantial volume of fresh water is added to the area except as river flow. MILLER (1952) obtained eighteen returns of bottles released on or near the 20 fathom contour in our area A. Their average drift was about 3·5 miles per day. The drift bottles, of course, do not give an evaluation of the movement of the deeper waters, but it seems probable that the surface drifts are greater than the average. Thus a maximum estimate of the advection of fresh water into the area can be made assuming that the water at all depths within the twenty fathom contour is passing from area A to area B at this velocity. The appropriate cross-section area is $3{\cdot}52 \times 10^6 \text{ ft}^2$, so that the total volume transport would be $7{\cdot}5 \times 10^{10} \text{ ft}^3/\text{day}$. Since the fresh water content ranges from 7·98–8·40%, the corresponding transport of fresh water would be $5{\cdot}6\text{–}6{\cdot}3 \times 10^9 \text{ ft}^3/\text{day}$. This includes the river water discharged directly into area A from the rivers emptying into Long Island Sound (Table II, Group A) which accounts for about one-fifth of the total gaged drainage, or about $2{\cdot}9 \times 10^9 \text{ ft}^3$ per day. Including the remainder,

$3{\cdot}4 \times 10^9$ ft^3/day, in the total river flow used in calculating the flushing times, would decrease them from about 1·6 years to 1·3 years—a change which is not significant considering the other approximations which have been made.

One tacit assumption has been made in the calculation of the horizontal mixing coefficients which has not been discussed. It is assumed that the current produced by the escaping river water is the only advective process of importance. Other currents, such as density and wind-induced currents, are also present. From the continuity of volume, the net transport of these currents must be zero, but it does not follow that the net transport of salt and fresh water must be zero. If, as seems likely, there are one or more large scale, counter clockwise eddies over the shelf, with an onshore current in the northern, low salinity, part of the region, and an offshore current in the southern higher salinity area, there will be a net offshore transport of salt. This would result in an underestimate of the coefficients of horizontal eddy diffusion. Unfortunately, our knowledge of the currents over the continental shelf, except for the narrow coastal strip, is inadequate to evaluate this effect.

A brief discussion of some of the forces which could produce the turbulence over the shelf may be of some interest. The tidal transport, the winds, the currents due to river flow and density structure, and the upwelling along the coast as a result of offshore winds, are the most obvious turbulent forces. In estuaries the mixing process has been related to the tidal volumes moving over a mixing length determined by the excursion of the tidal currents (ARONS and STOMMEL, 1951; KETCHUM, 1951). The approximate contribution of tidal flow over the continental shelf to the overall mixing process can be evaluated. For turbulent flow, the mixing effect would be proportional to the product of the velocity and the transport distance ($v_x l_x$). The coefficient of proportionality will vary, depending upon the actual degree of turbulence resulting from the flow, but the potential effect will always be less than this product. Both velocity and transport distance depend on the shape of the bottom contour and distance from shore, and the product will be greatest where the ratio of distance from shore to depth is a maximum (FLEMING, 1938). This product has been calculated for various depth contours for a semidiurnal tide with a mean amplitude of 50 cm, and has the following values, which may be compared with the coefficients of eddy diffusion listed in Table V.

30 fathoms	$0{\cdot}65 \times 10^6$ cm^2/sec.
40 fathoms	$1{\cdot}08 \times 10^6$ cm^2/sec.
100 fathoms	$0{\cdot}32 \times 10^6$ cm^2/sec.

This product increases to a maximum value at the 40 fathom contour and decreases beyond this depth, whereas the mixing coefficients decreased with increasing depth throughout this range. The tidal mixing product is always less than the coefficients of horizontal diffusion and the coefficient of proportionality is probably much less than unity. It may be concluded that the tides alone can contribute only a small fraction of the total turbulence, and that the other forces must contribute substantially at all times of year.

REFERENCES

ARONS, A. and STOMMEL, H. (1951), A mixing-length theory of tidal flushing. *Trans. Amer. Geophys. Union*, **32** (3), 419–421.

BIGELOW, H. B. (1913), Oceanographic cruises of the U.S. Fisheries Schooner *Grampus* 1912–1913. *Sci.* N. S. **38** (982), 599–601.

BIGELOW, H. B. (1915), Exploration of the coast water between Nova Scotia and Chesapeake Bay, July and August 1913 by the U.S. Fisheries Schooner *Grampus*. Oceanography and plankton. *Bull. Mus. Comp. Zool.* **59** (4), 151–359.

BIGELOW, H. B. (1927), Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.* **40** (2), 511–1027.

BIGELOW, H. B. (1933), Studies of the continental shelf, Cape Cod to Chesapeake Bay. 1. The cycle of temperature. *Pap. Phys. Oceanogr. Meteorol.* 2 (4), 1–135.

BIGELOW, H. B. and SEARS, M. (1935), Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. II. Salinity. *Pap. Phys. Oceanogr. Meteorol.* **4** (1), 1–94.

BOWDEN, K. F. (1950), Processes affecting the salinity of the Irish Sea. *Roy. Astron. Soc., Geophys. Supp.* **6** (2), 63–90.

FLEMING, R. H. (1938), Tides and tidal currents in the Gulf of Panama. *J. Mar. Res.* **1**, 192–206.

HAIGHT, F. J. (1938), Currents in Narragansett Bay, Buzzards Bay and Nantucket and Vineyard Sounds. U.S. Dept. of Commerce, Coast and Geodetic Survey, Spec. Publ. No. 208, 108 pp.

ISELIN, C. O'D. (1936), Study of the circulation of the north Atlantic Ocean. *Pap. Phys. Oceanogr. and Meteorol.*, **4** (4), 1–101.

ISELIN, C. O'D. (1940), Preliminary report on long-period variations in the transport of the Gulf Stream system. *Pap. Phys. Oceanogr. Meteorol.*, **8** (1), 1–40.

KETCHUM, B. H. (1951), The exchanges of fresh and salt waters in tidal estuaries. *J. Mar. Res.*, **10** (1), 18–38.

KETCHUM, B. H., REDFIELD, A. C. and AYERS, J. C. (1951), The oceanography of New York Bight. *Pap. Phys. Oceanogr. Meteorol.*, **10** (1), 1–46.

MARMER, H. A. (1935), Tides and currents in New York Harbor. U.S. Dept. of Commerce, Coast and Geodetic Survey, Spec. Publ. No. 111, VII + 198 pp.

MILLER, A. R. (1952), A pattern of surface coastal circulation inferred from surface salinity-temperature data and drift bottle recoveries, W.H.O.I., *Ref.* No. 52–28 (unpublished manuscript).

REDFIELD, A. C. and WALFORD, L. A. (1951), A study of the disposal of chemical waste at sea. *Nat. Res. Counc., Nat. Acad. Sci., Publ.* 201, 49 pp.

STOMMEL, H. (1953), Computation of pollution in a vertically mixed estuary. *Sewage Indust. Wastes*, **25** (9), 1065–1071.

SVERDRUP, H. U. and FLEMING, R. H. (1941), The waters off the coast of southern California, March to July, 1937, *Scripps Inst. Oceanogr. Bull.* **4**, 261–378.

SVERDRUP, H. U., JOHNSON, M. and FLEMING, R. H. (1942), The Oceans. Prentice Hall, Inc., New York, pp. 1–1087.

U.S. GEOLOGICAL SURVEY (1946), Surface water supply of the United States, Part 1, North Atlantic Slope Basins. *U.S. Dept. of Int. Geol. Surv. Water-Supply Paper* 1051, XIII + 676 pp.

U.S. NAVY HYDROGRAPHIC OFFICE (1946), Current atlas of the north Atlantic Ocean. (First ed.). *H.O. Misc.* No. 10688.

ZESKIND, L. M. and LELACHEUR, E. A. (1926), Tides and currents in Delaware River and Bay, *U.S. Dept. of Commerce, Coast and Geodetic Survey, Spec. Publ.* No. 123, 122 pp.

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Report on the results of exploratory otter-trawling along the continental shelf and slope between Nova Scotia and Virginia during the summers of 1952 and 1953*

By William C. Schroeder

Summary—No large fish populations were found comparable to those present on our known fishing banks.

The area designated as A, from Long. 63° 17′ to Long. 65° 59′ W, yielded considerably more fish both in number and pounds than did any of the areas from Long. 66° to Long. 74° 15′ W. The 200–400 fathom depth zone, on the overall average, produced the best catches throughout all these areas.

A total of 75 species of bottom dwelling fishes were caught, most of them in numbers so small as to suggest that they are of little economic importance within this region.

Among the dominant species were (*a*) the redfish, *Sebastes marinus*, which was taken in promising numbers, and large in size, in depths of 220–370 fathoms between Long. 63° 50′ and Long. 65° 27′ W; (*b*) the long-finned hake, *Urophycis chesteri*, found chiefly between 200–450 fathoms throughout all the areas fished; (*c*) the offshore hake, *Merluccius albidus*, taken west of Long. 66° and chiefly in 100–350 fathoms and (*d*) the grenadier, *Coryphaenoides rupestris*, present in greatest abundance east of Long. 66° and in depths of 300–500 fathoms.

Lobsters were caught in relatively large numbers off southern New England between 70–150 fathoms and as deep as 260 fathoms. A deep water lobster fishery in this region has ensued as a result of the discovery of these grounds.

The red crab, *Geryon quinquidens*, was found to be distributed throughout the range of our exploratory trawling in depths beyond 150–200 fathoms and in quantities that might prove sufficient to support a new fishery for this species which up to the present has been unexploited.

Bottom temperatures in 200–730 fathoms, throughout the region explored, varied but little either up and down the slope or from east to west, indicating a stability in this respect so far as concerns the bottom- and near bottom-dwelling marine life.

INTRODUCTION †

In the early 1880's the U.S. Fish Commission Str. *Fish Hawk* made a number of cruises to explore the bottom fauna along the southern New England coast, particularly in depths beyond 50 fathoms. Up until that time very little was known of the bottom dwellers of the outer shelf and the middle and upper slope of this region. However, the *Fish Hawk*, using a beam trawl, made about 100 successful hauls in depths ranging down to about 600 fathoms along a belt some 5 to 15 miles wide and extending about 150 miles from east of Nantucket to the offing of eastern Long Island. Here a rich fish and invertebrate fauna was found including many rare and previously

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* Contribution No. 790 of the Woods Hole Oceanographic Institution.

† This Introduction is somewhat repetitious to that given in "Deep water elasmobranchs and chimaeroids from the northwestern Atlantic Slope" (Bigelow and Schroeder, 1954, pp. 38 39.

unknown species. In this same period a number of bottom hauls were made still deeper along the slope, beyond 800 fathoms, by the *Blake* and the *Albatross*. It was just before these cruises, in 1879, that the tilefish had been discovered within this region. But, although various published reports appeared subsequently dealing with these catches, no organized deep water exploratory fishing was done along our northeastern Atlantic coast during the following seventy years, except a few stations made by the *Albatross* at widely separated times up until 1920.

The Woods Hole Oceanographic Institution vessel *Caryn*, in 1948 and 1949, made a few short cruises along the slope off southern Nova Scotia and New England and, for the first time, an otter trawl was used here in depths as great as 460 fathoms, all the earlier fishing having been done with relatively small Blake trawls and beam trawls, both of which were attached to rigid frames. The *Caryn*, although not well adapted to this type of fishing, made a total of 20 successful otter trawl hauls between 100 and 460 fathoms, the deepest haul being limited by the capacity of the winch. Many interesting specimens of fish and invertebrates were taken.

It now seemed timely to explore more fully the outer part of the shelf and upper slope, not only to seek rare or little known species and to learn something about them ecologically, but to determine whether or not any fish or invertebrates were to be found there in quantities and of a sort that might be of interest to the commercial fishery; in other words, to locate new fishing grounds. Accordingly, *Cap'n Bill II*, an 83 ft. dragger built in 1952 in Thomaston, Maine, owned and captained by HENRY W. KLIMM, Jr., was chartered by the Woods Hole Oceanographic Institution for three cruises in June–July 1952 and three cruises in June–July 1953.

Up to the present time most of the bottom trawling done by the commercial fishing fleet along the Atlantic coast has been in less than 125 fathoms, although the redfish vessels have recently been operating near the southern part of the Grand Bank in depths approaching 200 fathoms. Beyond this extreme, most of the boats are not equipped to fish much deeper with otter trawls, being limited by the amount of wire that can be wound on the winches which they now carry. In the commercial fishery two wires, or warps, usually $\frac{3}{4}$ or $\frac{15}{16}$ inches in diameter, are used in fishing the trawls which are upwards of 100 feet wide at the mouth with otter boards each weighing from 700 to 2000 pounds or more. In our experimental fishing we used a single wire of $\frac{3}{8}$ inches with a 20-fathom bridle of $\frac{5}{16}$ inches reaching to the otter boards. In making our earlier hauls various types of boards were used, but during most of 1952 and all of 1953 a standardized type was employed, each board having a weight of 160 pounds. The trawls measured, respectively, 35, 50, and 60 feet at the foot rope, and about 18 per cent less at the head rope, with body and wings of 3 inch, 15 thread stretched mesh, and the cod end of $1\frac{1}{2}$ inch, 24 thread. Double $\frac{3}{16}$ inch galvanized chain was attached to the foot rope, and floats in varying number, to the head rope. Glass floats proved the most satisfactory for withstanding the great pressures beyond 300 fathoms, although some of them became partially filled with water and had to be replaced. Aluminium floats of the sort we used, were the least effective as most of them imploded beyond 200 fathoms.

The duration of the tows varied from one-half to one hour depending on depth, roughness of the bottom, and weather conditions. Fishing was done chiefly during daylight hours, but in some instances extended into late evening. In cases where long runs from one area to another were necessary, these were made at night without loss of fishing time. The towing speed averaged about 2½ knots. Bottom temperatures, recorded by a maximum-minimum thermometer, were obtained in 1953.

Six cruises were made, as follows:

Cruise No. 1: June 20 to June 27, 1952, from Hudson Canyon to the offing of Nantucket (Long. 72° 05′ to Long. 69° 37′ W); 50 hauls in depths ranging from 105 to 500 fathoms. Mr. JAMES BARKER accompanied me.

Cruise No. 2: July 10 to July 17, 1952, from the offing of Nantucket to the offing of Georges Bank (Long. 69° 37′ to Long. 67° 45′ W); 35 hauls in depths ranging from 75 to 530 fathoms. Dr. BENJAMIN LEAVITT accompanied me, as well as Dr. P. SCHOLANDER and DR. L. VAN DAM who took gas and blood samples of various species of fish to supplement their data for shoaler water.

Cruise No. 3: July 23 to July 30, 1952, from the offing of Georges Bank to the offing of southeastern Nova Scotia (Long. 66° 55′ to Long. 63° 17′ W); 32 hauls in depths ranging from 67 to 540 fathoms. Dr. RICHARD H. BACKUS assisted me, and Drs. SCHOLANDER and VAN DAM continued their work on gas and blood samples.

Cruise No. 4: June 25 to July 1, 1953, from the offing of Cape Charles, Virginia to Hudson Canyon (Long. 74° 15′ to Long. 72° 04′ W); 45 hauls in depths ranging from 63 to 720 fathoms. Dr. BENJAMIN LEAVITT participated in this cruise, and Drs. SCHOLANDER and VAN DAM continued their gas and blood studies.

Cruise No. 5: July 10 to July 17, 1953, from the offings of Georges Bank to southeastern Nova Scotia (Long. 65° 27′ to Long. 63° 47′ W); 31 hauls in depths ranging from 68 to 705 fathoms. Mr. ROBERT WOLF of U.S. Fish and Wildlife Service assisted me, while Drs. SCHOLANDER and VAN DAM continued their observations.

Cruise No. 6: July 23 to July 30, 1953, from the offings of Nantucket to Georges Bank (Long. 70° 43′ to Long. 66° 39′ W); 34 hauls in depths ranging from 70 to 730 fathoms. Mr. JAN HAHN accompanied me and made a photographic record of the trip.

Table I

A list of the total hauls, 32 of them by the Caryn *and 227 by the* Cap'n Bill II, *arranged by depths*

Fathoms	*Number of Hauls: Successful*	*Number of Hauls: Not Successful*
0–50	0	1
51–100	20	2
101–150	18	2
151–200	16	10
201–250	22	5
251–300	18	8
301–350	22	4
351–400	15	8
401–450	21	11
451–500	21	5
501–550	8	2
551–600	4	2
601–650	4	4
651–700	2	0
701–730	2	1
830–890	0	1
Total	193	66

In most cases the trawl fished bottom without apparent mishap, but there were occasions when a haul obviously was not successful for one reason or another, as is to be expected when fishing an unexplored area and in depths where technical difficulties are multiplied. Catch statistics of unsuccessful bottom hauls were segregated from those hauls considered representative.

The causes for the 66 unsuccessful or otherwise unrepresentative hauls were: trawl did not fish bottom at all or for only a small part of the haul (22); net tore so that all or part of the catch was lost (13); drawstring opened before catch was landed (1); net lost (9); gear twisted (13); aluminium floats all imploded (1); fathometer not operating (2); trawling wire snapped (2); cause unknown (3). Catch records of these hauls are not included in this report.

RESULTS

A total of 75 species of fishes that might be classed as dwelling part or all of the time on bottom, or close to it, were caught in the two years combined, of which 7 species were taken in 1952 only and 13 in 1953 only. These figures are subject to slight revision after a number of final indentifications have been established. In addition, some 30–40 species of bathypelagic fishes were captured while the trawl was being payed out and/or hauled in and when an off-bottom haul was made. These species have not yet been critically studied. Accounts of the sharks, skates and chimaeras taken deeper than 200 fathoms have already been published (BIGELOW, SCHROEDER and SPRINGER, 1953; BIGELOW and SCHROEDER, 1954) as well as a paper dealing with two fishes of especial interest, the offshore hake *Merluccius albidus* and the blue whiting *Gadus* (*Micromesistius*) *poutassou* (BIGELOW and SCHROEDER, 1955). Also, certain data concerning various fishes taken on these Atlantic slope cruises are included in recently published *Fishes of the Gulf of Maine* (BIGELOW and SCHROEDER, 1953).

Much the greater number of the bottom-dwelling species that were taken deeper than 200 fathoms are at present of little commercial importance, either because of their relative scarcity in deep water or because they have not yet been accepted as food fishes. In fact, only the redfish (*Sebastes marinus*) was found in numbers sufficient to give some promise of supporting a profitable fishery. Others taken that might prove of some value to the fisheries include the gray sole (*Glyptocephalis cynoglossus*), the long-finned hake (*Urophycis chesteri*) and the whitings (*Merluccius bilinearis* and *M. albidus*).

New and prolific lobster grounds were discovered and considerable information was obtained on the distribution and abundance of the deep water red crab (*Geryon quinquidens*), a species that may prove to form the basis of a new crab fishery.

As the area fished, although only about 5 to 20 miles wide, extended some 600 miles from the offing of Nova Scotia to that of Cape Charles, Virginia, it is expedient that it be divided into sectors, as follows: area A—Long. 63° 17′ to 65° 59° W, from the offing of southeastern Nova Scotia to the eastern slope of Georges Bank; area B—Long. 66° 00′ to 69° 59′ W, from the eastern slope of Georges Bank to the offing of Nantucket; area C—Long. 70° 00′ to 71° 59′ W, from the offing of Nantucket to Hudson Canyon; and area D—Long. 72° 00′ to 74° 15′ from Hudson Canyon to the offing of Cape Charles, Virginia. The most northerly latitude fished was 42° 48′, and the most southerly, 37° 38′ (see Fig. 1).

Table II

A list of the fish species taken by the Caryn *and the* Cap'n Bill II *arranged by areas, depths, hauls, and aggregate catches, in which 50 hauls were made in area A, 56 hauls in area B, 49 hauls in area C, and 38 hauls in area D*

Species	*Fathoms*		*Caught in*		*Number of fish: Aggregate catch*		
	— 200	+ 200	1–10 *Hauls*	11+ *Hauls*	1–10	11–100	101+
Myxine glutinosa	D		X		X		
Petromyzon marinus		A	X		X		
Scyliorhinus retifer	B–C–D		X			X	
Apristurus profundorum		A–B–C–D		X		X	
Mustelus canis	D		X		X		
Centroscymnus coelolepis		B–C–D	X		X		
Centroscyllium fabricii		A–B–C–D		X			X
Etmopterus princeps		A–B–C		X		X	
Raja bathyphila		B	X		X		
erinacea	B		X		X		
fyllae		A–B		X		X	
garmani	B–C–D			X		X	
jenseni		A D	X		X		
laevis	C	A–B–C	X		X		
mollis		A	X		X		
ocellata	B		X		X		
radiata	B–C	A–B–C–D		X		X	
senta	B–C–D	A–B–C–D		X		X	
spinicauda		A–B	X		X		
Harriotta raleighana		A–B–C–D		X		X	
Rhinochimaera atlantica		A–B D	X		X		
Argentina silus		A		X		X	
striata	A–B–C–D		X			X	
Notacanthus phasganorus		A C	X		X		
Polyacanthonotus rostratus		A	X		X		
Simenchelys parasiticus		A–B–C–D		X		X	
Conger oceanica	D		X		X		
Synaphobranchus pinnatus		A–B–C–D		X			X
Chlorophthalmus chalybeius	B–C–D	B–C–D		X			X
truculentus	B–C		X		X		
Merluccius bilinearis	A–B–C–D	A–B–C		X			X
albidus	B–C–D	B–C–D		X			X
Gaidropsarus ensis		A	X		X		
Enchelyopus cimbrius	C		X		X		
Pollachius virens	A		X		X		
Melanogrammus aeglefinis	A–B D		X				X
Antimora rostrata		A–B–C–D		X			X
Urophycis regius	B–C–D			X			X
tenuis	B–C–D	A–B–C–D		X			X
chuss	A–B–C–D			X			X
chesteri	B–C–D	A–B–C–D		X			X
Laemonema barbatulum		D	X		X		
Brosme brosme		A	X		X		
Gadus (Micromesistius) poutassou		A–B	X		X		
Macrourus bairdii	B–C–D	A–B–C–D		X			X
berglax		A–B		X		X	
Coelorhynchus carminatus	B–C–D	B–C–D		X			X
Coryphaenoides rupestris		A–B–C–D		X			X
Citharichthys arctifrons	B–C–D			X			X
Monolene sessilcaudata	C–D		X			X	
Reinhardtius hippoglossoides		A–B		X		X	
Hippoglossus hippoglossus		A	X		X		

Table II (continued)

Species	*Fathoms*		*Caught in*		*No. of fish Aggregate catch*		
	— 200	+ 200	1–10 *Hauls*	11+ *Hauls*	1–10	11–100	101+
Hippoglossoides platessoides	A	A	X		X		
Paralichthys oblongus	B–C–D	B		X			X
Glyptocephalus cynoglossus	B–C–D	A–B–C–D		X			X
Zenopsis ocellatus	D		X		X		
Polymyxia nobilis	C–D		X			X	
Poronotus triacanthus	B–C–D		X			X	
Lopholatilus chamaeleonticeps	C		X		X		
Sebastes marinus	A	A–B–C		X			X
Helicolenus dactylopterus	B–C–D	B–C–D		X			X
Myoxocephalus octodecemspinosus	A		X		X		
Cottunculus microps		A–B		X		X	
thompsoni		A–B–C–D		X		X	
Paraliparis copei		A–B	X			X	
Peristedion miniatum	B–C–D			X			X
Tautogolabrus adspersus	B		X		X		
Macrozoarces americanus	B		X		X		
Lycodes esmarkii		B	X		X		
frigidus		A–B–C	X		X		
Lycenchelys paxillus		A	X		X		
Dicrolene intronigra		B–C–D		X		X	
Lepophidium cervinum	C–D		X		X		
Lophius americanus	A–B–C–D	A–B–C–D		X		X	
Dibranchus atlanticus	B–C–D	A–B–C–D		X			X

Thus the 193 hauls yielded only 21 species of which the aggregate catch was greater than 100 individuals, 21 species which ranged from 11 to 100, and 33 species from 1 to 10.

It is not surprising that most of our commercial species, including haddock, pollock and various flounders, were not taken as deep as 200 fathoms, for their known depth range does not extend that far. On the other hand, the total absence of cod in our hauls, and the capture of only 1 cusk and of 1 halibut deeper than 200 fathoms, indicate that they are much too scarce along the northwestern Atlantic slope, within the scope of our exploratory trawling, ever to support or contribute materially to a fishery there. While cod are not taken in substantial numbers deeper than 200 fathoms, in fact about 125 fathoms marks the ordinary limit in our fishery, the cusk descends to 250–300 fathoms (though most plentiful considerably shoaler), and the halibut to 400–500. It is possible that a scarcity of preferential food and type of bottom may be chiefly responsible for this paucity of cusk and halibut along the slope. On the other hand, temperature, *per se*, does not seem to be a limiting factor; for the 38°–42° which exists throughout the year all along the route of our exploratory fishing, in 200–500 fathoms, is a favourable range for both these species.

While the shoaler water fishes (those which we caught above 200 fathoms and no deeper) are included in the preceding table, species other than those listed are known to be present in winter but not in summer within this depth range—notably the spiny dogfish (*Squalus acanthias*), the summer flounder (*Paralichthys dentatus*), the scup

(*Stenotomus versicolor*) and the sea robin (*Prionotus carolinus*), all of which I have seen taken in large numbers by commercial fishermen in mid-winter off southern New England, within the 50–100 fathom zone. On the other hand it is difficult to explain our capture of only one tilefish (*Lopholatilus*) for, while the population appears to be more scattered during the summer, it is a year around resident in about 60–150 fathoms, most abundantly between the offings of Nantucket and Delaware Bay where draggers, from late fall to spring, often take 10–20,000 pounds per trip. Certainly there is evidence here that some species may easily evade the small trawls such as were used in our exploratory fishing.

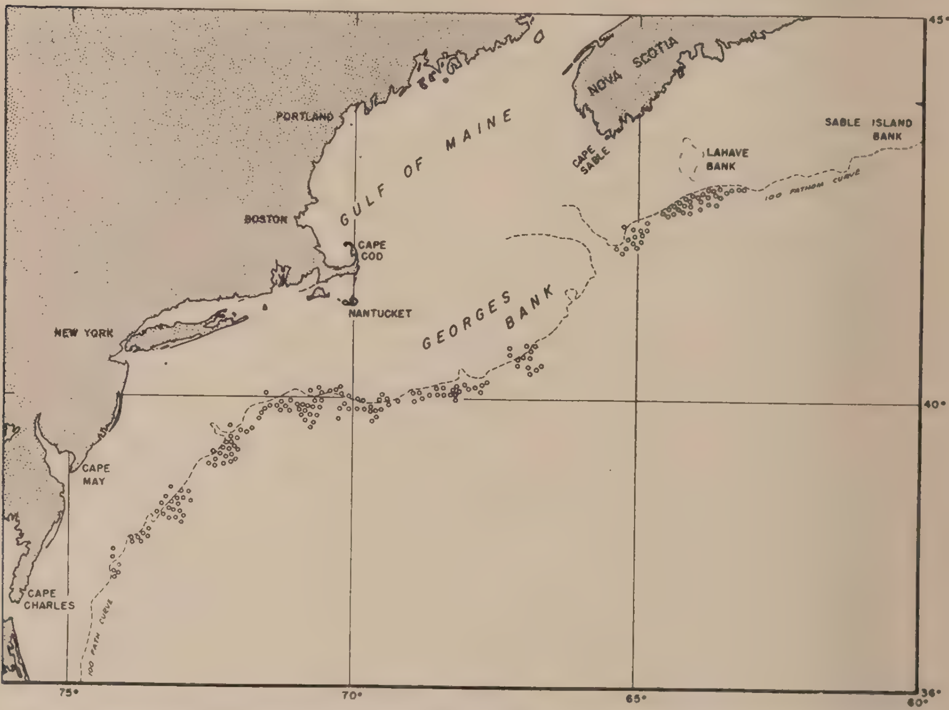
PORTLAND
GULF OF MAINE
NOVA SCOTIA
CAPE SABLE
SABLE ISLAND BANK
LAHAVE BANK
100 FATHOM CURVE
BOSTON
CAPE COD
NANTUCKET
GEORGES BANK
NEW YORK
CAPE MAY
CAPE CHARLES
100 FATH CURVE
45°
40°
36°
75°
70°
65°
60°

Fig. 1. Distribution of bottom otter-trawling stations along the shelf and slope made during June–July 1952 and 1953 by *Cap'n Bill II.*

In this connection it is of interest to note the difference in yield between our 50 foot and the 60 foot trawls in such cases where they could be reasonably compared for the same depth zone and area. Thus in 53 hauls of the 50 foot trawl, 16,618 fish of all sorts estimated to weigh about 9,500 pounds were caught, or an average of 314 fish and about 180 pounds per haul, while the catch in 33 hauls of the 60 foot trawl was 12,316 fish estimated to weigh about 11,500 pounds, or an average of 373 fish and about 350 pounds per haul. The larger trawl not only caught more fish by number (as might be expected) but also fish that averaged larger in size . Much the same result was obtained in the catch of crabs (*Geryon*), for in 31 hauls of the 50 foot trawl the average catch per haul was 32 crabs weighing about 40 pounds, while in 21 hauls of the 60 foot trawl the average catch was 41 crabs weighing about 60 pounds, in areas and depths where the catches could be reasonably compared.

These data are presented to emphasize the importance of giving due consideration

Table III

Catch by depth zones and areas giving the total number of hauls and the average number and estimated weight of fish caught per haul of 1 hour, in depths greater than 100 fathoms

Fathoms	Area A			Area B			Area C			Area D			Average		
	Hauls	*Number*	*Pounds*	*Hauls*	*Number*	*Pounds*	*Hauls*	*Number*	*Pounds*	*Hauls*	*Number*	*Pounds*	*Hauls*	*Number*	*Pounds*
101–200	(0)			(8)	216	107	(13)	371	207	(9)	386	185	(30)	333	168
201–300	(10)	900	1013	(9)	408	192	(9)	261	180	(5)	450	258	(33)	522	447
301–400	(16)	1053	710	(2)	321	180	(5)	273	204	(5)	180	90	(28)	705	471
401–500	(9)	929	480	(2)	200	113	(0)			(4)	338	150	(15)	674	345
501–730	(6)	683	488	(3)	135	105	(2)	230	165	(8)	158	93	(19)	327	226
Average	(41)	933	700	(24)	285	150	(29)	311	190	(31)	300	153			

to the type of gear used when interpreting results quantitatively and qualitatively. It is a matter for speculation as to what our catches would have been had larger trawls been employed.

In the preceding table the catches of all the fishes taken during 1952–1953, deeper than 100 fathoms (excluding bathypelagic species), are segregated by depths and areas and converted to a standard based on the 60 foot trawl dragged on bottom for 1 hour.

According to this summary the greatest number and poundage of fish, taken together, was found between 200 and 400 fathoms, and the species contributing most to this were the redfish (*Sebastes*) and a macrourid (*Coryphaenoides*) in area A, the offshore hake (*Merluccius albidus*) in areas B, C, D, and the long-finned hake (*Urophycis chesteri*) in areas A, B, C, D.

The upper hundred fathoms of the slope (100–200 fathoms) produced the smallest yield in pounds of fish per haul, while deeper than 400 fathoms the decline was apparent, and here a substantial part of the catch comprised the macrourids (*Macrourus bairdii* and *Coryphaenoides rupestris*), the long-finned hake, and the gray sole (*Glyptocephalus*). Along the outer part of the shelf, in 50–100 fathoms (not included in Table III) the 20 hauls made averaged only about 100 fish weighing 50 pounds.

A 60 foot trawl having a footrope about 50 ft. wide, fishing a swath estimated to be 30 ft. wide in a one-hour drag at 2½ knots, would traverse an area equal to about 10½ acres.

Table IV
Calculated catch of fish in pounds per acre

Fathoms	*Area A* *Pounds*	*Area B* *Pounds*	*Area C* *Pounds*	*Area D* *Pounds*	*Average* *Pounds*
101–200	(no hauls)	10·2	19·7	17·6	16
201–300	96·5	18·3	17·1	24·6	43
301–400	67·6	17·1	19·4	8·6	45
401–500	45·7	10·8	(no hauls)	14·3	33
501–730	46·5	10·0	15·7	9·0	22
Average*	67	14	18	15	

* Based on the total number of hauls as given in Table III.

Thus Table IV (which presents in another form part of the data in Table III) shows that area A, from Long. 63° 17′ W to 65° 59′ W, was considerably more productive in pounds of fish per acre than areas B, C, or D, from Long. 66° W to 74° 15′, which were rather uniform in yield as compared one with the other.

These figures of yield per acre would be increased considerably by the use of a commercial-size otter trawl. And the amounts would have been substantially greater (regardless of trawl size) if our efforts had been directed chiefly in exploiting the most productive grounds rather than in exploring poor areas as well. From the standpoint of the food-fish fishery the most promising region is in area A between 200 and 400 fathoms where *Sebastes* was dominant, and for the so called trash-fish fishery areas A to D in this same depth zone, together with areas C–D in 100–200 fathoms and area A in 400–730 fathoms.

So few records are available pertaining to the yield of fish per acre on the ocean bottom that it is of interest to note here data obtained during 1936 for a small area in the Gulf of Maine to the westward of Jeffrey's Ledge where, in 80–100 fathoms, using an 82 foot shrimp trawl calculated to fish a breadth of 52 ft., the catch of fish per acre worked out to about 47 pounds.*

There follows a further discussion of certain of the species listed in Table II (p. 362) arranged by groups.

ELASMOBRANCHS AND CHIMAEROIDS

The species comprising this group, caught deeper than 200 fathoms, have been discussed by BIGELOW and SCHROEDER (1954). Only the black dog-fish (*Centroscyllium fabricii*) was taken in relatively large numbers, chiefly in 300–550 fathoms within area A.

EELS

Of the several species of Apodes caught, the long-nosed eel *Synaphobranchus pinnatus* was the most plentiful, chiefly in area A between 450 and 500 fathoms, where the best 4 hauls averaged about 150 of this species. In areas B, C, and D, where it was found to be much less plentiful, the best catches likewise were made in the 450–500 fathom zone. The shoalest capture was in 220 fathoms, beyond which it was taken at all depths down to our deepest haul at 730 fathoms.

CODS AND HAKES

Both in numbers and poundage this group proved dominant in depths beyond 200 fathoms. Most plentiful is the long-finned hake *Urophycis chesteri*, taken in small numbers as shoal as 125 fathoms and as deep as 730 fathoms, with the best catches between 200 and 450 fathoms. For example, in area A 2 hauls averaged 676 hake in 200–250 fathoms, and 8 hauls averaged 360 hake in 250–300 fathoms; in area B the average of 3 hauls was 267 in 250–300 fathoms, in area C 6 hauls averaged 125 in 200–250 fathoms, and the best hauls in area D were 2 averaging 254 hake in 250–300 fathoms. The general run of fish ran 1–1½ pounds.

Moderate numbers of blue hake, *Antimora rostrata*, were taken in area A between 300–700 fathoms, the average catch per haul ranging from 14 to 29 individuals, while in areas B, C and D a scattering few were caught between 400–730 fathoms. In size the general run ranged from 10 to 14 inches, the extremes from 6 to 21½ inches.

The red hake, *Urophycis chuss*, important chiefly in the inshore trash-fish fishery, and the white hake, *U. tenuis*, considered of more value as a food fish, were taken in scattering numbers throughout areas A to D, the former down to 200 fathoms and the latter to 550 fathoms.

An account of the first western Atlantic records of the blue whiting *Gadus* (*Micromesistius*) *poutassou* is given by BIGELOW and SCHROEDER (1955). One specimen was trawled on the seaward slope of Georges Bank, Lat. 40° 18′ N, Long. 68° 01′ W at 230–250 fathoms, July 15, 1952 and three others at 240–280 fathoms on the slope of Browns Bank between Lat. 42° 09′ N Long. 65° 21′ W and Lat. 42° 08′ N, Long. 65° 27′ W, July 16 1953. They ranged in standard length from 349 to 416 mm.

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* See BIGELOW and SCHROEDER (1939) p. 322, where the catch of shrimp and fish is given as 55 pounds per acre, of which the fish comprised about 85 per cent, or 47 pounds per acre.

The offshore hake, *Merluccius albidus*, was next in importance, but none at all was taken in area A. In the other areas a scattering few were caught as shoal as 55–100 fathoms and deeper than 400 fathoms, but the best yields were as follows: area B, an average of 80 to 108 per 5 hauls between 200–350 fathoms; area C, 126 to 400 per 3 hauls between 150–350 fathoms; area D, 140–164 hake per 14 hauls in 100–300 fathoms. The majority of these hake ranged from 1 to 3 pounds, some as large as 4–4½ pounds.

The silver hake, *M. bilinearis*, an important shoal water commercial species, was not found to be an important factor off shore. The best catches were in area B, where in 100–300 fathoms an average of 70 to 125 fish was taken in 6 hauls.

GRENADIERS OR MACROURIDS

More pounds of *Coryphaenoides rupestris* were taken than of any other macrourid, chiefly because of its relatively large size (most of those taken ranged from 1 to 6 pounds) and its abundance within area A where, between 300–550 fathoms, the averages for 36 hauls ranged from 220 to 535 fish of this species. The shoalest capture was in the 200–250 fathom zone, and the deepest around 700 fathoms. To the westward, within areas B, C, and D, relatively few were taken, and these deeper than 350 fathoms, the best catch being an average of 70 fish in 2 hauls made in area D in 450–500 fathoms.

The common grenadier or rat-tail, *Macrourus bairdii*, was found to be very widespread in all depths from 150 fathoms to 730 (our deepest haul) throughout areas A to D. The better catches (between 300–700 fathoms) ran from about 75 to 150 fish per haul. But as this species averages only ¼–½ pound in weight, the poundage taken per haul was insignificant.

THE FLOUNDER TRIBE

The gray sole (*Glyptocephalus cynoglossus*) is the only flounder that was found to be widespread deeper than 200 fathoms. In fact, it was caught in a greater number of hauls than any other species of fish listed in Table II. On the other hand, although it was widespread, no large concentrations were found, and the general range in size was relatively small, only about ¼ to 1 pound, with but few reaching 2 pounds or more. This flounder was taken just about everywhere between 120 and 730 fathoms from areas A to D. Excluding the smallest catches, the results were: Area A, 200–550 fathoms, 23 to 96 fish per haul; area B, 250–600 fathoms, 17 to 45 fish per haul; area C, 150–730 fathoms, 18 to 120 fish per haul; area D, 150–730 fathoms, 12 to 114 fish per haul. The greatest number taken in a single haul was 218, area A, 350–400 fathoms.

It is of interest to note that the gray sole is one of the important food fishes in the northern Atlantic where, off our coast, the best catches are made between about 60 and 150 fathoms.

Only 1 halibut was caught during our exploratory fishing, this a 75 lb. fish taken in 340–360 fathoms in Lat. 42° 41′ N, Long. 63° 58′ W. The paucity of halibut along the slope is referred to on p. 363.

A few Greenland halibut (*Reinhardtius hippoglossoides*) were taken, 20 of them between Long. 63° 47′ and 65° 10′ (area A) and 1 at 67° 59′ (area B), this latter being the most westerly known record. The depth range was 305–530 fathoms, the size from 13 to 36 inches long.

REDFISH OR OCEAN PERCH

Although the redfish occurs in great abundance in the North Atlantic, especially off New England, Nova Scotia and the Grand Banks, virtually all of our catch was taken within area A. A list follows of those hauls in which more than 100 redfish were caught:

Table V

Catches of Sebastes marinus *taken between Long.* 63° 17′ *and Long.* 65° 59′ W, *converted to a* 1 *hour haul with a* 60 *ft. otter trawl, arranged by longitude*

Station	*Date*	*Lat.*	*Long.*	*Fathoms*	*Redfish* *Number*	*Redfish* *Bushels*	*Bottom** *Temp. F.*
164	July 12, 1953	42° 43′	63° 50′	310–335	210	6½	39·4
173	July 13, 1953	42° 40′	64° 10′	240–270	450	15	40·3
105	July 27, 1952	42° 41′	64° 13′	260–290	386	9¾	
172	July 13, 1953	42° 36′	64° 15′	220–370	744	25	39·6
176	July 14, 1953	42° 33′	64° 17′	280–320	189	6¾	40·1
184	July 15, 1953	42° 23′	64° 52′	265–295	728	28	40·1
188	July 15, 1953	42° 17′	65° 01′	270–340	720	24	39
109	July 28, 1952	42° 20′	65° 03′	305–320	510	17	
189	July 15, 1953	42° 18′	65° 05′	220–240	338	11¼	40·5
191	July 16, 1953	42° 09′	65° 21′	240–280	1056	32	40
193	July 16, 1953	42° 08′	65° 27′	250–300	298	9	39

* As a maximum-minimum thermometer was used the temperatures given are presumed to be for the deepest part of a haul.

All of these fish ranged in length from 12 to 19 inches with a mean of about 15 to 16 inches, with the exception of one of 8½ inches. The count in most cases ran from 30 to 35 fish to the bushel. Thus the populations sampled proved to contain exclusively very large redfish and, according to present age studies, such fish were probably from 15 to 20 years old.

A ready explanation as to why virtually no small or medium redfish were taken in these hauls is not available at the present time. True, this area had never been fished before with otter trawls, so far as is known, and therefore being a virgin territory might be the answer, at least in part. And it is of interest to note that the Fisheries Research Board of Canada engaged in exploratory dragging for redfish in the Gulf of St. Lawrence during 1953 and 1954, and found areas in 100–175 fathoms where the dominant sizes of the fish likewise were very large, ranging from 35 to 40 cm. (14 to 16 inches).† On the other hand, the newly exploited redfish grounds in the Grand Banks region where trawlers have been operating as deep as 175 fathoms, and perhaps a little more, have from the beginning produced a substantial percentage of small to medium fish.

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† MARTIN in *Fish. Res. Bd., Canada, Rept. Atlantic Biol. Sta. for* 1953 (1954), pp. 61–64, and STEELE and MARTIN in *Fish. Res. Bd., Canada, Rept. Atlantic Biol. Sta. for* 1954 (1955), pp. 63–65.

No hauls were made in 100–200 fathoms in area A, but it appears certain that redfish occur there along the upper slope, perhaps in somewhat the same abundance as they are at present found on the slope of the Grand Banks. But it is not likely that any large bodies of fish are to be found deeper than about 370 fathoms in area A (Long. 63° 17′ to Long. 65° 59′ W), for only 11 were caught in 27 hauls made there in 400–700 fathoms, the deepest catch being at about 425.

While our best catches of redfish were taken within the narrow temperature range of 39°–40·5° F, they are known to occur in more or less abundance between about 36° and 48°, with the 38°–42° temperature zone probably the most favourable for it.* But factors other than temperature influence the presence and abundance of redfish, of which type of bottom and an adequate supply of preferred food (chiefly euphausiids, shrimps, small mollusks and various other invertebrates) must play an important part, as only a scattering few were taken by us in the many hauls made along the slope to the westward of Long. 66° in temperatures of 38°–42°.†

The black-bellied rosefish (*Helicolenus dactylopterus*), a close relative of the redfish, was taken in small numbers in areas B, C, D, between 70 and 300 fathoms, the best catches being in 150–200 fathoms with averages per haul as follows: area B, 66 fish in 3 hauls; area C, 160 fish in 8 hauls, and area D, 87 fish in 2 hauls. The usual size was 6–8 inches in length, the extreme range 3–13 inches.

MISCELLANEOUS SPECIES

Of the remaining species listed in Table II, and not otherwise mentioned, there follows the depth ranges of those which were captured beyond 200 fathoms in this survey, the deepest haul made being in 730 fathoms.

Table VI
Depth range of fish not otherwise mentioned

Species	*Range in Fathoms*
Petromyzon marinus	220–470
Argentina silus	200–380
Notacanthus phasganorus	270–570
Polyacanthonotus rostratus	220–370
Simenchelys parasiticus	250–730
Chloropthalmus chalybeius	50–250
Gairdropsarus ensis	415–545
Antimora rostrata	300–730
Laemonema barbatula	275–650
Macrourus berglax	250–530
Coelorhynchus carminatus	100–460
Hippoglossoides platessoides	265–295
Paralichthys oblongus	50–235
Cottunculus microps	200–500
Cottunculus thompsoni	250–700
Lycodes esmarkii	400–430
Lycodes frigidus	350–520
Lycenchelys paxillus	250–480
Dicrolene intronigra	450–730
Lophius americanus	50–450
Dibranchus atlanticus	150–500

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* For a more detailed account see BIGELOW and SCHROEDER 1953, p. 432.

† See STEELE and MARTIN (1955), who trawled large redfish in the Gaspé region in 39·4°–40·9°, and who point out that the presence and abundance of the euphausiid *Meganyctiphanes norvegica* appeared to be an important factor determining the distribution and movements of redfish.

It is probable that some of the *Argentina* and *Chloropthalmus* were taken well off bottom. Most of the species listed above are known from depths beyond those given here. None were taken in large numbers.

LOBSTERS AND RED CRABS

It is planned to present in a separate paper, an account of the lobsters (*Homarus americanus*) and red crabs (*Geryon quinquidens*) taken during this exploratory fishing. It can be said here that lobsters were found in quantities sufficient to support at least a limited amount of commercial fishing in depths of from about 70 to 150 fathoms where we trawled up to 4 bushels or more in a 1 hour drag between Long. 69° 30′ and Long. 71°. Catches also were made as deep as 260 fathoms and as far westward and southward as fishing was done (Lat. 37° 38′ N, Long, 74° 15′ W.)

It has long been known that lobsters, especially very large ones, occur off shore between the offings of Nova Scotia and North Carolina, and in the last few years otter trawlers have been bringing in fair catches from off the coast of New Jersey. But since releasing information concerning their whereabouts and relative abundance off the New England coast, based on our recent investigations, a number of boats have been operating successfully with catches reported as high as 8,000 pounds landed from a 5- or 6-day trip. All sizes of lobsters are present in this offshore area from about 5 inches in total length to those weighing 20 pounds or more. While the average size has been considerably larger than that taken inshore by the trap fishery, in which the size of the trap opening excludes large lobsters, nevertheless a good proportion of very small ones is present also. There is an indication from this that the offshore population, rather than being composed chiefly of large and very old individuals that may have gradually worked into deeper water, is in fact made up substantially of all ages. It would seem therefore that the offshore stock is not too dependent on emigrants from inshore but rather that much of this population owes its existence to lobsters being carried there during their planktonic existence.

The red crabs were found throughout the areas fished, but while they were taken in the deepest hauls their shoalest range was quite sharply defined. Thus in area A they first appeared at about 250 fathoms, in areas B and C at about 200 fathoms, and in area D at about 150 fathoms. The best average catches per 1 hour drag were as follows: area A, 23 to 115 crabs in 300-550 fathoms; area B, 30 to 79 in 200–400 fathoms; area C, 29 to 80 in 200–550 fathoms, and area D, 65 to 203 crabs in 150–450 fathoms. They were well distributed, for catches were made in almost every haul made within these depths.

In size the great majority of the red crabs ranged from 1 to 2 pounds and, as they have proven very good to eat, there is a possibility that a fishery for them may develop.

BOTTOM TEMPERATURES

On the three cruises made in 1953, from June 25 to July 30, temperatures were obtained for most of the hauls with a maximum-minimum thermometer which was attached to an otter board. It may be presumed that these minimum temperatures, in most cases at least, were those prevailing at or very close to the bottom.

It must be admitted that the instruments used were not of a quality or calibration comparable to the precision of the best deep-sea reversing thermometers. However, from time to time the latter were used as a check on the former, and differences in

Table VII

The average temperatures in °F for various depths in the four sub-areas with the number of stations or hauls shown in parentheses

Fathoms	*Area A* 63° 17′–65° 59′	*Area B* 66° 00′–69° 59′	*Area C* 70° 00′–71° 59′	*Area D* 72° 00′–74° 15′
101–125	–	(1) 53	(2) 50·8	(2) 47·8
126–150		(1) 45		(4) 46·8
151–200	(3) 42·7		(1) 46	(2) 46
201–250	(1) 40·5	(3) 41·3	(1) 42	(1) 42·4
251–300	(7) 40	(1) 40·5		(3) 40·6
301–350	(5) 39·1	(1) 40		(2) 40·1
351–400	(3) 39·6	(1) 40	(1) 39	(4) 39·7
401–450	(2) 39·6	(2) 38·5		(3) 39
451–500	(3) 39·1	(3) 39		(2) 39·2
501–550	(2) 39·7			(3) 39
551–600		(1) 38	(1) 39·6	(2) 38·8
601–650	(2) 39·7	(2) 39·7		(3) 38·7
651–700				(2) 38·9
701–730	(1) 38	(1) 39	(1) 38·5	(2) 38·8

temperature between the two were seldom greater than 0·5°. It is of interest to note, also, that the results listed above agree very closely with those obtained in the same region, in summer, by the *Blake*, *Fish Hawk* and *Albatross* in the 1880's.

As we are concerned here chiefly with conditions along the Atlantic slope, within the region explored, as it pertains to the bottom-dwelling fishes and other marine life, it seems evident that the temperatures at or near bottom, between 200 and 730 fathoms at least, are very uniform. And while this applies to June–July, the few readings obtained by the *Albatross* in February–March 1920 between Long. 64° and 68° W in 200–700 fathoms are in close agreement.

So far as the role of temperature, *per se*, is concerned with the presence and abundance of these fishes living beyond 200 fathoms, conditions appear to be very stable, and it would not be surprising if the results thus far obtained, with due consideration to the type and efficiency of the gear employed, would be found to be approximately the same for any season or year. Only further exploratory work can reveal whether or not this is so.

REFERENCES

Bigelow, Henry B. and Schroeder, William C. (1939), Notes on the fauna above mud bottoms in deep water in the Gulf of Maine. *Biol. Bull.*, **76** (3), 305–324.

Bigelow, Henry B. and Schroeder, William C. (1953), Fishes of the Gulf of Maine. *Fish. Bull.* 74, *Fish and Wildlife Serv.*, **53**, 1–577.

Bigelow, Henry B. and Schroeder, William C. (1954), Deep water Elasmobranchs and Chimaeroids from the northwestern Atlantic Slope. *Bull. Mus. Comp. Zool., Harvard Coll.*, **112** (2), 37–87.

Bigelow, Henry B. and Schroeder, William C. (1955), Occurrence off the middle and north Atlantic United States of the offshore hake *Merluccius albidus* (Mitchill) 1818, and of the blue whiting *Gadus* (*Micromesistius*) *poutassou* (Risso) 1826. *Bull. Mus. Comp. Zool., Harvard Coll.*, **113** (2), 205–226.

Bigelow, Henry B., Schroeder, William C. and Springer, Stewart (1953), New and little known sharks from the Atlantic and from the Gulf of Mexico. *Bull. Mus. Comp. Zool., Harvard Coll.*, **109** (3), 213–276.

Martin, W. R. (1954), Redfish ecology in the Gulf of St. Lawrence. In: *Fish. Res. Bd., Canada, Rept. Atlantic Biol. Sta. for* 1953, 61–64 (unpublished manuscript).

Steele, D. H. and Martin, W. R. (1955), Redfish ecology in the Gaspé area. In: *Fish .Res. Bd., Canada, Rept. Atlantic Biol. Sta. for* 1954, 63–65 (unpublished manuscript).

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 373-397.

Stromgeschwindigkeiten im Tiefen- und Bodenwasser des Atlantischen Ozeans auf Grund dynamischer Berechnung der *Meteor*—Profile der Deutschen Atlantischen Expedition 1925/27

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Summary—This new dynamic study of the *Meteor* profiles (German Atlantic Expedition, 1925–27) is based on the " dynamic reference surface " of Defant (1941), which admittedly is only a first approximation. It is particularly concerned with the current velocities of the deep and bottom water of the Atlantic Ocean. Selected transverse profiles, longitudinal sections and charts indicate unexpectedly large measurable current velocities in the axis of the North Atlantic Deep Current and of the Antarctic Bottom Current flowing along the foot of the continental slope off South America. On the average, these have a velocity of 9·2 and 7·2 cm/sec, and reach maximal velocities of 17·4 and 12·5 cm/sec. These calculated current velocities are probably not too high because of the great distances between stations along the profiles.

The sources of error of the dynamic method are discussed. It appears reasonable to believe that a useful approximation has actually been determined.

EINLEITUNG

Nichts kann den unbefriedigenden Stand unserer Kenntnisse über die Stromgeschwindigkeiten in der Tiefsee besser beleuchten als das Urteil eines so erfahrenen Ozeanographen wie G. E. R. Deacon (1954), der folgendes schreibt: " We have known for 150 years that there is water, nearly ice-cold, at the bottom of the tropical Atlantic Ocean, and that it must flow there from the Antarctic, but we can still argue whether it took 18 years or 1800, and there is as much uncertainty about the forces which move it there." Diese Ungewissheit rührt daher, dass es bisher weder durch direkte Strommessungen auf Ankerstationen noch durch indirekte Methoden der Berechnung oder Schätzung gelungen ist, die kontinuierlichen Wasserbewegungen in den Tiefen von mehr als 2500 m nach Richtung und Geschwindigkeit genügend genau zu erfassen und damit zu einer brauchbaren quantitativen Lösung des Zirkulationsproblems zu gelangen. Hinsichtlich der Strommessungen auf Ankerstationen hat kürzlich K. F. Bowden (1954) gezeigt, dass " direct measurements have provided a comparatively small portion of our knowledge of subsurface currents in the oceans " und betont, dass es eine vordringliche Aufgabe der ozeanographischen Forschung sei, mit verbesserten Methoden und Instrumenten—wenn möglich völlig unabhängig von jeder Eigenbewegung des Schiffes und über jeweils etwa 1 Woche—die mittleren Strömungen und ihre nicht-periodischen Schwankungen in der Tiefsee zu messen. Denn nur auf diesem Wege vermöge man—so argumentiert Bowden weiter—, die mit anderen, indirekten Methoden " geschätzten " Werte der ozeanischen Tiefenzirkulation zu verifizieren, nur so könne man zu zuverlässigen Werten gelangen, die nicht nur für die Ozeanographie, sondern auch für die Meeresgeologie und die marine Biologie der Tiefsee im Hinblick auf die Bearbeitung der Sedimentprobleme und der Probleme der Verbreitung der Organismen so unentbehrlich sind.

Bei dieser Sachlage erscheint eine erneute dynamische Bearbeitung der *Meteor*—Profile 1925/27, wie sie vom Verfasser im folgenden in Angriff genommen ist und welche die Berechnung der absoluten Stromkomponenten und der transportierten Wassermengen senkrecht zu den Profilen in den Tiefen zwischen der DEFANT'schen Bezugsfläche (Nullfläche) und dem Tiefseeboden zum Ziel hat, durchaus geboten. Denn nur auf diese Weise besteht Aussicht, die von A. DEFANT (1936 A) und G. WÜST (1936) gewonnenen Vorstellungen räumlich und in quantitativer Richtung zu erweitern und zu fundieren.* Bei der Berechnung der zahlreichen Tabellen und der Eintragung der Werte in mehr als 30 grosse dynamische Profile und Karten, die später in extenso an anderer Stelle veröffentlicht werden sollen, habe ich mich der sorgfältigen Hilfe durch Herrn cand. rer. nat. E. NOODT erfreut.

RÜCKBLICK AUF DIE BISHERIGEN INDIREKTEN SCHÄTZUNGEN DER STROMGESCHWINDIGKEIT

Die Bedeutung unserer neu berechneten Werte der Stromgeschwindigkeit wird erst ersichtlich, wenn wir sie in Beziehung stellen zu den bisherigen Ergebnissen der nicht sehr zahlreichen Versuche, auf indirekte Weise zu Schätzungen bzw. Näherungswerten dieses Faktors für die Tiefsee zu gelangen. Aus diesem Grunde sei ein kurzer Rückblick vorausgeschickt, wobei hinsichtlich der Geschichte der allgemeinen, d.h. mehr qualitativen Erforschung der Ausbreitung des atlantischen Tiefen- und Bodenwassers auf die ausführlichen Darstellungen des Verfassers im *Meteor*—Werk (1933 und 1936) verwiesen werden kann.

Die ersten Versuche von FORCH (1911), THOULET (1921, 1925), WATTENBERG (1927), DEACON (1931), CASTENS (1931, 1932) und SEIWELL (1939) haben heute im wesentlichen nur historische und rechnerische Bedeutung, da die ihnen zugrundeliegenden Annahmen bzw. Voraussetzungen, wie im *Meteor*- Werk dargelegt worden ist, in der Tiefsee nicht erfüllt sind. So hat der Verfasser (1933, S.55) gezeigt, dass " es verfehlt ist, in der Temperaturzunahme des antarktischen Bodenstroms von Süden nach Norden in der Westmulde und Ostmulde einen sichtbaren Effekt der Erdwärme zu erblicken und aus dieser Temperaturzunahme und dem annähernd bekannten vom Erdinnern ausgehenden Wärmestrom etwa die Geschwindigkeit des Bodenstroms berechnen zu wollen ", wie es C. FORCH (1911) versucht hat. Denn " diese Zunahme der Temperatur beruht, wie die Kurven lehren, ganz überwiegend auf dem Vorgang der Vermischung " (WÜST 1933, S.55). Auch THOULETS (1921; 1925) beharrliche Auffassung von der Bewegungslosigkeit der Wassermassen in den Tiefen von mehr als 2000 m ist heute überholt. Denn " gerade im untersten Stockwerk des Ozeans sind die Wassermassen in der Temperatur und im Salzgehalt wesentlich stärker differenziert als in der darüberliegenden Tiefenschicht, verharren keineswegs in Bewegungslosigkeit, sondern befinden sich offenbar in der Mehrzahl der Tiefseebecken in merklich strömender Bewegung, die wir unmittelbar aus dem Verlauf der Isothermen ablesen können " (WÜST 1933, S.34). Andererseits hat der Verfasser (1936, S. 182–201) durch eine kritische Prüfung hinsichtlich der von WATTENBERG (1927) vermuteten jahreszeitlich bedingten Schwankungen von Salzgehalt, Sauerstoff und Temperatur in den Kernschichten des subantarktischen Zwischenwassers und des nordatlantischen Tiefenwassers klargestellt, dass aus den Beobachtungen des *Meteor* keine klar definierten räumlichen Unterschiede dieser 3 Faktoren im " Stromstrich " der Kernschichten nachweisbar sind, die mit Sicherheit auf jahreszeitlich bedingte, periodische Einflüsse in den Absinkgebieten zurückgeführt werden und dazu dienen können, die Geschwindigkeiten der Ausbreitung dieser Wasserarten zu berechnen. So erweist sich leider auch dieser originelle von Wattenberg (1927) geäusserte Gedanke, der dann von Deacon (1931), Castens (1931, 1932) und Seiwell (1934) aufgegriffen worden ist, nicht als realisierbar, zumal anzunehmen ist, " dass unperiodische Schwankungen eine grössere Rolle spielen, als man bisher im allgemeinen annimmt " (Wüst 1936, S.193), eine Vermutung, die durch eine neuere Untersuchung von Worthington (1954) gestützt wird. Wattenberg (1935) hat noch einen anderen, ebenfalls recht interessanten Weg zur Berechnung des Massenaustausches über dem Tiefseeboden und damit zur Berechnung der Geschwindigkeit des antarktischen Bodenstroms beschritten. Aus der Zunahme der spez. Alkalinität längs seinem Vordringen im Brasilianischen Becken, d.h. aus der Abgabe des aus dem Sediment gelösten Kalziumkarbonats berechnet er zunächst den vertikalen Austauschkoeffizienten A zu $4\ \text{cm}^{-1}\ \text{g}\ \text{sec}^{-1}$. Unter Benutzung des von A. Defant (1935) zu 4–9 abgeleiteten Verhältnisses A : c kommt Wattenberg (1935) zu dem Ergebnis, " dass eine mittlere Geschwindigkeit (c) von 0·5 bis 1 cm/sek im Antarktischen Bodenstrom einen hohen Grad von Wahrscheinlichkeit besitzt", was in guter Übereinstimmung stehe mit dem von H. Mosby (1934) geschätzten Wert von 1 cm/sek. In der definitiven Bearbeitung der " Ausbreitungs- und Vermischungsvorgänge im antarktischen Bodenstrom und im subantarktischen Zwischenwasser " berechnet A. Defant (1936 b) erneut aus den vom Verfasser konstruierten Längsschnitten der potentiellen Temperatur und des Salzgehalts in den Bodenschichten auf der Westseite des Atlantischen Ozeans die Grösse des Verhältnisses A : c in den einzelnen Tiefen und Zonen und gelangt unter Annahme des Wattenbergschen Austauschwertes A = 4 zu folgenden Geschwindigkeitswerten* im *Hauptstromstrich des antarktischen Bodenstroms*:

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* Die Durchführung dieser umfangreichen Untersuchung, von der mit Genehmigung des Herausgebers der Wissenschaftlichen Ergebnisse der Deutschen Atlantischen Expedition, Herrn Prof. Dr. A. DEFANT, hier eine erste Mitteilung vorgelegt wird, ist dem Verfasser durch die Bewilligung einer Sachbeihilfe seitens der Deutschen Forschungsgemeinschaft ermöglicht worden, wofür aufrichtig gedankt sei.

über den Schwellen zwischen 1·5 und 2 cm/sek
über den Mulden zwischen 0·5 und 1 cm/sek.

Für den Stromstrich des *unteren nordatlantischen Tiefenstroms* erhält er auf diese Weise Geschwindigkeitswerte zwischen 0·3 und 0·8 cm/sek. Die eingehende Analyse der Ausbreitung und Vermischung der Wassermassen in der atlantischen Kaltwassersphäre mittels der Kernschichtmethode hat den Verfasser (Wüst 1936, S.243) zu der Erkenntnis geführt, " dass bei allen 5 Wasserarten von meridionalen Komponenten und einem stromartigen Charakter der Ausbreitung nur ganz auf der Westseite des Ozeans gesprochen werden kann. In die östlicheren Regionen werden die Wasserarten durch zonale Ausbreitung, ja stellenweise entgegengesetzte Bewegungen bzw. durch ganz allmähliche Einwirbelung verfrachtet ". Und an anderer Stelle: " Denn die Verbreitung der verschiedenen Wasserarten im Ozeanraum ist nicht identisch mit der wahren Bewegung im Raume. Nur in den Achsen der Kernmassen kann durch Pfeile die Richtung der Tiefwasserbewegungen dargestellt werden ”. In einer zusammenfassenden Darstellung seiner verschiedenen Untersuchungen über “ Bodentemperatur und Bodenstrom in der atlantischen, indischen und pazifischen Tiefsee ” hat sich der Verfasser (WÜST 1938 B) schliesslich auch der Frage der absoluten Geschwindigkeiten im Stromstrich des antarktischen Bodenstroms zugewandt. Unter der unbewiesenen Annahme, dass in der oberen Hälfte der Grenzschicht zwischen dem Tiefen- und dem Bodenwasser, bei der in der atlantischen Westmulde vielfach (besonders im Argentinischen und Brasilianischen Becken) “ geradezu von einer Sprungschicht der Temperatur und des Salzgehalts zwischen 3500 und 4500 m Tiefe ” (WÜST 1933, S.70) gesprochen werden kann, die dynamische Bezugsfläche zu suchen ist, hat diese damalige vorläufige dynamische Bearbeitung von 9 *Meteor*- Querprofilen zwischen 55° S und 5° S für den Stromstrich zu Nordkomponenten im Betrage von 0·8 bis 4·0 cm/sek, im Durchschnitt 2·2 cm/sek geführt. DEFANT (1941) hat es aber in seiner umfassenden Bearbeitung des atlantischen Massenfeldes auf Grund von 629 Stationen sehr wahrscheinlich gemacht, dass die dynamische Bezugs- oder Nullfläche nicht identisch ist mit solchen Grenz—bzw. Sprungschichten, sondern dass sie nur aus dem Massenaufbau des Meeres ermittelt werden kann und zwar als *die* Schicht, in welcher die Differenzen der dynamischen Tiefen zwischen benachbarten Stationen praktisch konstant sind und daher die Wasserversetzungen als sehr nahe Null angenommen werden dürfen. Natürlich ist sich DEFANT (1941) darüber im klaren, dass es zunächst nur “ eine reine Annahme ist, wenn man nun innerhalb dieser Schicht die Bezugsfläche zur Überführung der relativen Topographien der Druckflächen in absolute legt ”. DEFANT (1941, S.242) fährt fort: “ aber die Annahme gewinnt sofort an grosser Wahrscheinlichkeit und innerer Sicherheit, wenn man bemerkt, dass die für einzelne Stationspaare bestimmten Lagen der Bezugsfläche sich in ein in sich geschlossenes System zusammenfügen, wenn man den ganzen Ozean betrachtet.” Eine wesentliche Stütze sieht DEFANT ferner in der inneren Übereinstimmung seiner Stromfelder der stationären Konvektionsströme mit den Ausbreitungskarten der verschiedenen Wasserarten, welche der Verfasser mittels der Kernschichtmethode unter Eintragung von Pfeilen der Hauptausbreitung 1936 abgeleitet hat. Aus einem Überblick über die “ Fernwirkungen antarktischer und nordatlantischer Wassermassen in den Tiefen des Weltmeeres ”, in welchem der Verfasser (1951) in vereinfachter Form die DEFANTschen Stromkarten für 800 und 2000 m Tiefe und die diesen Niveaus am nächsten kommenden Ausbreitungskarten der Kernmassen des subantarktischen Zwischenwassers und des mittleren nordatlantischen Tiefenwassers gegenübergestellt hat, geht diese grosse innere Übereinstimmung der beiden voneinander unabhängigen Methoden besonders klar hervor. In der 2000-decibar-Fläche findet DEFANT in der ganzen Westhälfte des Ozeans—ganz in Übereinstimmung mit den Ergebnissen der Kernschichtmethode—vorwiegend meridionale Strömungen nach Süden, welche das in den grönländischen Gewässern abgesunkene sauerstoffreiche Tiefenwasser auf direktem Wege bis nach 30°–40° S verfrachten mit mittleren Geschwindigkeiten im Stromstrich ganz auf der Westseite von 2 cm/sek und maximalen von 7 cm/sek. Nur in der Querschnittsverengung am Äquator vor Kap San Roque werden nach DEFANT Stromstärken von 8 bis 14 cm/sek erreicht. Seit 1941 sind dem Verfasser keine weiteren Berechnungen von Stromgeschwindigkeiten in der Tiefsee bekannt geworden ausser einem kühnen und summarischen Versuch von G. A. RILEY (1951), die *mittleren* Geschwindigkeiten der Nord- und Südkomponenten zwischen 0 und 4000 m und in den verschiedenen geographischen Breiten, gemittelt jeweils über die *ganze* Breite des Ozeans, zu berechnen. Für 4000 m Tiefe gibt RILEY Mittelwerte zwischen 0·01 und 0·08 cm/sek an, Werte, die für unsere Problemstellung, die auf die absoluten Geschwindigkeiten im Stromstrich des nordatlantischen Tiefenstroms und des antarktischen Bodenstroms abzielt, keine Bedeutung besitzen.

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* Hiermit hat Defant (1936 b) die in seiner vorläufigen Mitteilung (1935) auf die gleiche Weise für den Bodenstrom berechneten Geschwindigkeiten, die " zwischen 1 und 5 cm/sek liegen, im allgemeinen aber kaum 10 cm/sek übersteigen dürften ", als zu hoch gekennzeichnet.

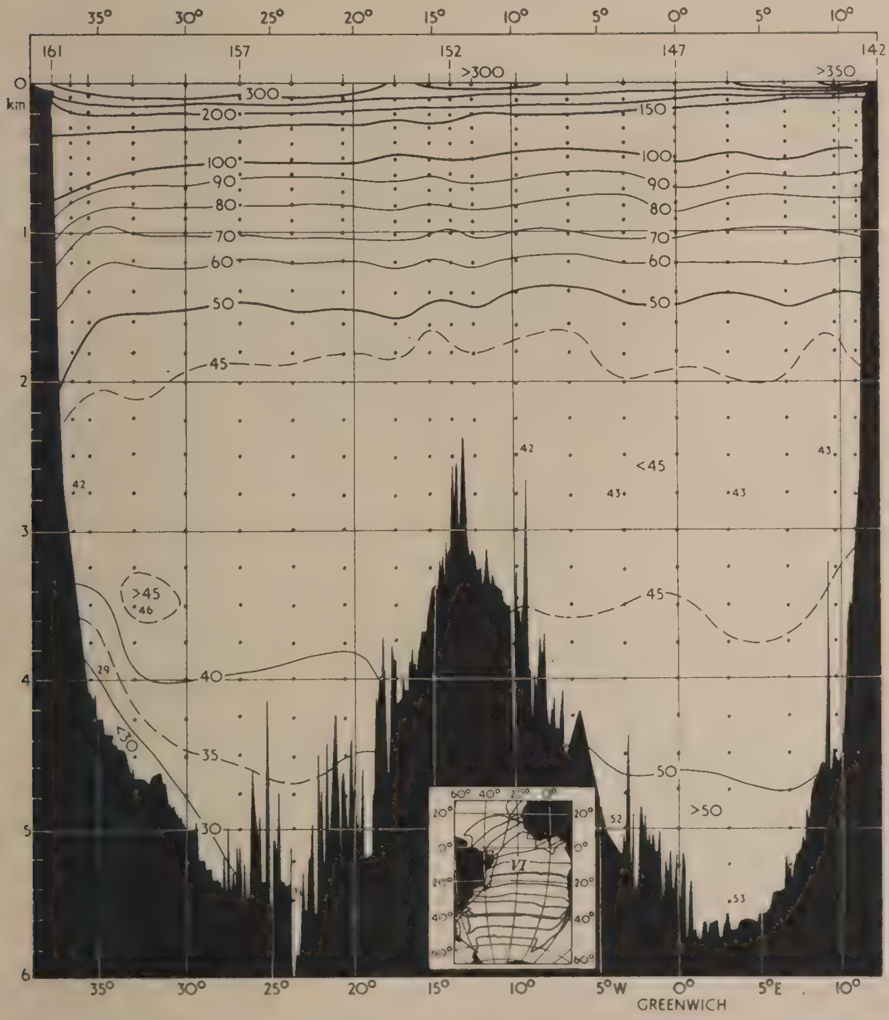


Fig. 1. Vertikalschnitt der Anomalien des spezifischen Volumens $\delta = 10^5 (\alpha - \alpha_{35}, 0, p,)$. *Isosteren-Schnitt*, " *Meteor* "—*Profil VI* (Mai–Juni 1926) durch das Brasilianische und das Angola-Becken in 15°–18° S.

DIE DYNAMISCHE BEARBEITUNG DER *METEOR*- PROFILE

Unsere neue dynamische Untersuchung knüpft—besonders im Hinblick auf die Topographie der dynamischen Bezugsfläche—an die Untersuchung DEFANTS (1941) über " die absolute Topographie des physikalischen Meeresniveaus und der Druckflächen, sowie die Wasserbewegungen im Atlantischen Ozean " an und erweitert sie auf die Schichten zwischen 2500 m Tiefe und dem Tiefseeboden, jedoch mit dem durch die geringere Beobachtungsdichte gegebenen Unterschied, dass wir nicht eine Lösung für den Gesamtraum, d.h. nicht die Konstruktion von geschlossenen Stromfeldern für die einzelnen Niveaus wie Defant anstreben. Wir beschränken uns vielmehr auf die Stromkomponenten senkrecht zu den *Meteor*- Profilen und versuchen lediglich, für den Hauptstromstrich des Tiefen- und Bodenstroms ganz auf der Westseite des Ozeans die berechneten Werte der Stromstärke auf die " wahre " Stromrichtung zu reduzieren. Die wesentlichen Grundlagen unserer Berechnungen sind durch die Werte der Anomalien des spezifischen Volumens $\delta = 10^5 \, (\alpha - \alpha_{35,0,p})$ gegeben, wie sie in den " Listen der dynamischen Werte für die Standardhorizonte an den Beobachtungsstationen " des Forschungsschiffes *Meteor* vom Verfasser (1938 A) veröffentlicht sind. Jedoch erweist es sich für unsere Aufgabe als erforderlich, ab 2500 m Tiefe nach unten den Abstand der Standardtiefen—durch vertikale und horizontale Interpolationen und Kontrollen mittels der im Atlas zu Band VI enthaltenen Vertikalschnitte und Horizontalkarten von t°, $S^\circ/_{\circ\circ}$ und σ_t (Wüst, 1936)—grundsätzlich auf 250 m zu verringern und möglichst bis zum Tiefseeboden zu erweitern, um die wahrscheinlichen Werte der Anomalien des spezifischen Volumens für unsere dynamische Berechnung einsetzen zu können, besonders im Bereich der submarinen Steilabfälle des Meeresbodens. Denn nur auf diese Weise ist es möglich, die von Helland-Hansen (1934) angegebene Methode der " Fortsetzung der Berechnung in Gebiete geringerer Tiefe " anzuwenden. Die nunmehr zwischen 0 und 1000 m Tiefe für alle 100 m, zwischen 1000 und 2000 m Tiefe für alle 200 m und zwischen 2000 m Tiefe und dem Tiefseeboden für alle 250 m Tiefenabstand vorliegenden Werte δ (der Anomalien des spezifischen Volumens) haben wir für alle *Meteor*- Profile in Vertikalschnitte grossen Masstabs eingetragen und durch eine möglichst engabständige Konstruktion der Isosteren (für alle 5 Einheiten unterhalb $\delta = 50$) noch einmal kontrolliert und in ihrer räumlichen Verteilung festgelegt. Hierdurch ist eine genügend gesicherte Extrapolation zum Tiefseeboden und die Fortführung der dynamischen Berechnung in Gebiete geringerer Tiefe nach der Methode Helland-Hansens gegeben. In Fig. 1 und 2 sind als Beispiele in starker Verkleinerung die zwei Isosteren—Vertikalschnitte für die *Meteor*- Profile VI (15°–18° S) und I (40°–42° S) reproduziert. In beiden Schnitten erkennen wir zunächst die grosse Zahl von Fixpunkten, welche der Isosterenkonstruktion zugrundeliegen und dann die bemerkenswerte Drängung und Schrägstellung der Isosteren zwischen 3000 m und 5000 bzw. 5500 m Tiefe in der Westmulde, was uns schon darauf hinweist, dass die Höchstzahl der Solenoide nicht in der Kältezunge der Westmulde, sondern links von ihr ganz am Westrande des Brasilianischen und des Argentinischen Beckens gelegen ist. Ganz anders liegen die Verhältnisse in den grossen Tiefen der ostatlantischen Mulde. Hier bestehen noch bemerkenswerte Unterschiede zwischen dem Angola-Becken (nördlich des Walfischrückens) und dem Kap-Becken (südlich davon). Während ansonsten die Anomalien des spezifischen Volumens mit der Tiefe abnehmen, wachsen sie in dem (durch den Walfischrücken gegen den antarktischen Bodenstrom) abgeriegelten Angola-Becken ab ca. 3000 m mit der Tiefe, so dass hier am Boden δ – Werte > 50 existieren, gegenüber < 30 bzw. 25 im Westen, wo sich also am Fusse des

Kontinentalabfalls jeweils die absoluten Minima der Anomalien der spezifischen Volumina innerhalb der Vertikalschnitte befinden.

Mittels des so verdichteten Netzes von Fixpunkten sind für alle *Meteor*- Profile zwischen den benachbarten Stationen zunächst die Werte von $A = -\int v dp$, d.h. die Anzahl der Solenoide berechnet und aus diesen unter Berücksichtigung der geographischen Breite φ und des Abstandes L zwischen den Stationen die Geschwindigkeitsdifferenzen $c_0 - c_1$ — unter Weglassung der Stationspaare, die zwischen 4° N und 4° S gelegen sind—ermittelt, und zwar nach der bekannten Formel von Helland-Hansen und Sandström, die auf der Bjerknesschen Zirkulationstheorie beruht:

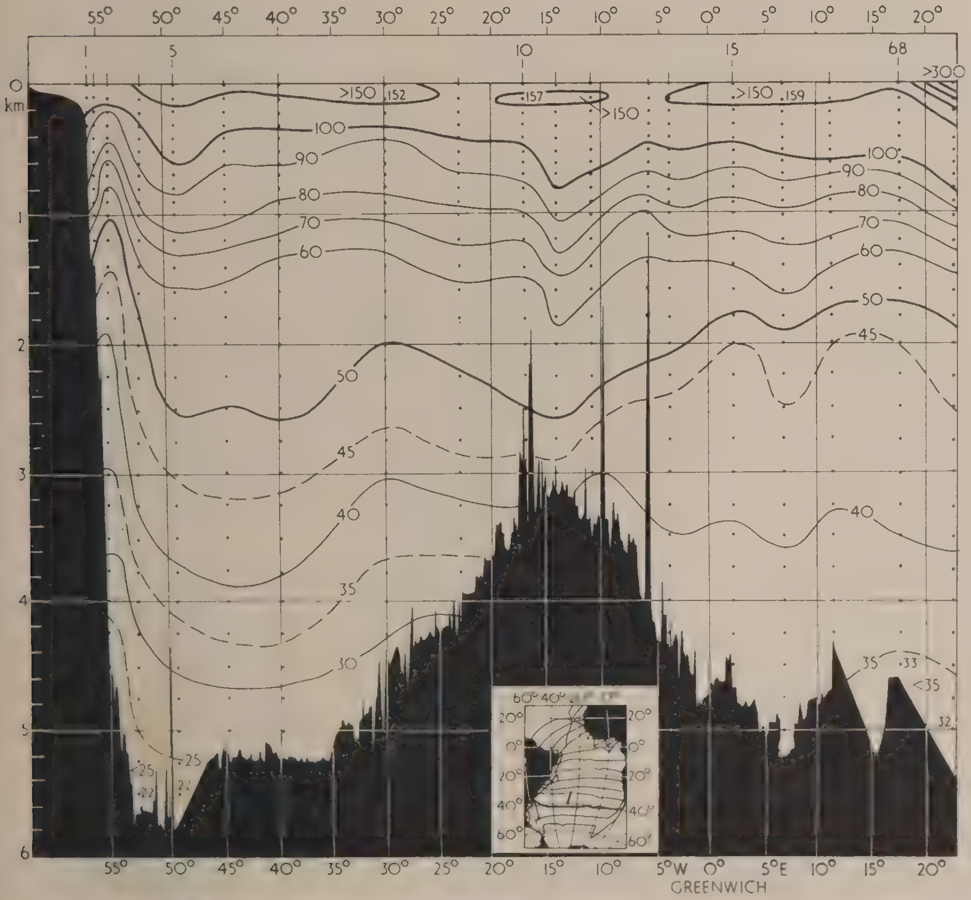


Fig. 2. Vertikalschnitt der Anomalien des spezifischen Volumens $\delta = 10^5 (\alpha - \alpha_{35}, 0, p.)$. *Isosteren-Schnitt,* "*Meteor*"- *Profil I* (Juni–Juli 1925) durch das Argentinische und das Kap-Becken in 40°–42° S.

$$c_0 - c_1 = \frac{A}{2w \, . \, L \, . \, \sin \varphi}$$

Die für jedes Stationspaar gültige dynamische Bezugsfläche D_0 ist sodann aus Defants Karte der " Tiefenlage der Bezugsfläche zur Ermittlung der absoluten Topographie der einzelnen Isobarenflächen " (1941, Beilage XIX), welche Isobasen für alle 100 m enthält, auf 1 Hektometer genau entnommen und der Berechnung der absoluten Stromgeschwindigkeiten c_1 zugrundegelegt worden. Diese Werte c_1 stellen die Geschwindigkeitskomponenten des stationären Konvektionsstroms senkrecht

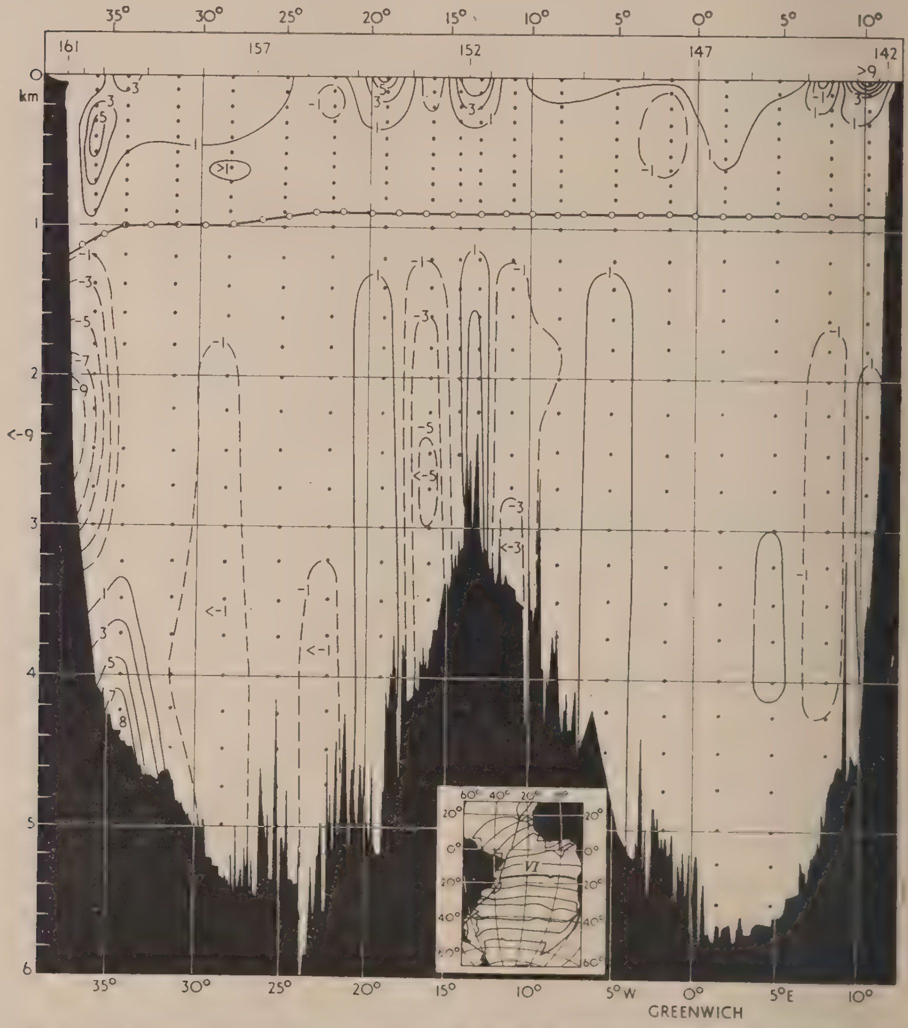


Fig. 3. Vertikalschnitt der berechneten *Geschwindigkeitskomponenten* (cm/sek) senkrecht zum " *Meteor* "—*Profil VI* (Mai–Juni 1926) durch das Brasilianische Becken und das Angola-Becken in 15°–18° S.

nördliche Komponenten ausgezogene Isotacheen,
südliche Komponenten gestrichelte Isotacheen,
–O–O–O–O– dynamische Bezugsfläche n. Defant (1941).

zu den *Meteor*- Profilen dar, bezogen auf die ganze Strecke zwischen zwei Stationsvertikalen. Dadurch, dass nach den Plänen von A. MERZ (1925) die Querprofile des *Meteor* über den Ozean senkrecht zu den wichtigsten ozeanischen Böschungen der Kontinentalabfälle und des Atlantischen Zentralrückens angelegt worden sind, bestehen von vornherein günstige Voraussetzungen für die Anwendung des *Bjerknes*schen Verfahrens; denn sowohl Theorie als Beobachtung lehren, dass das Relief

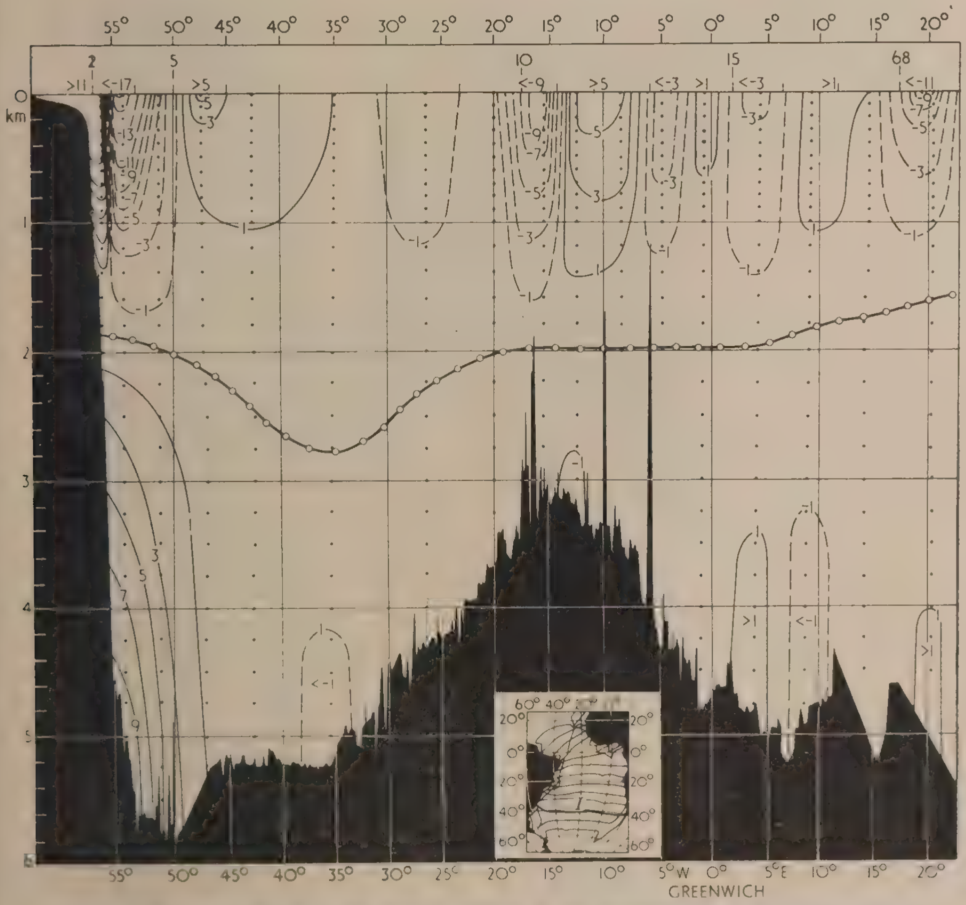
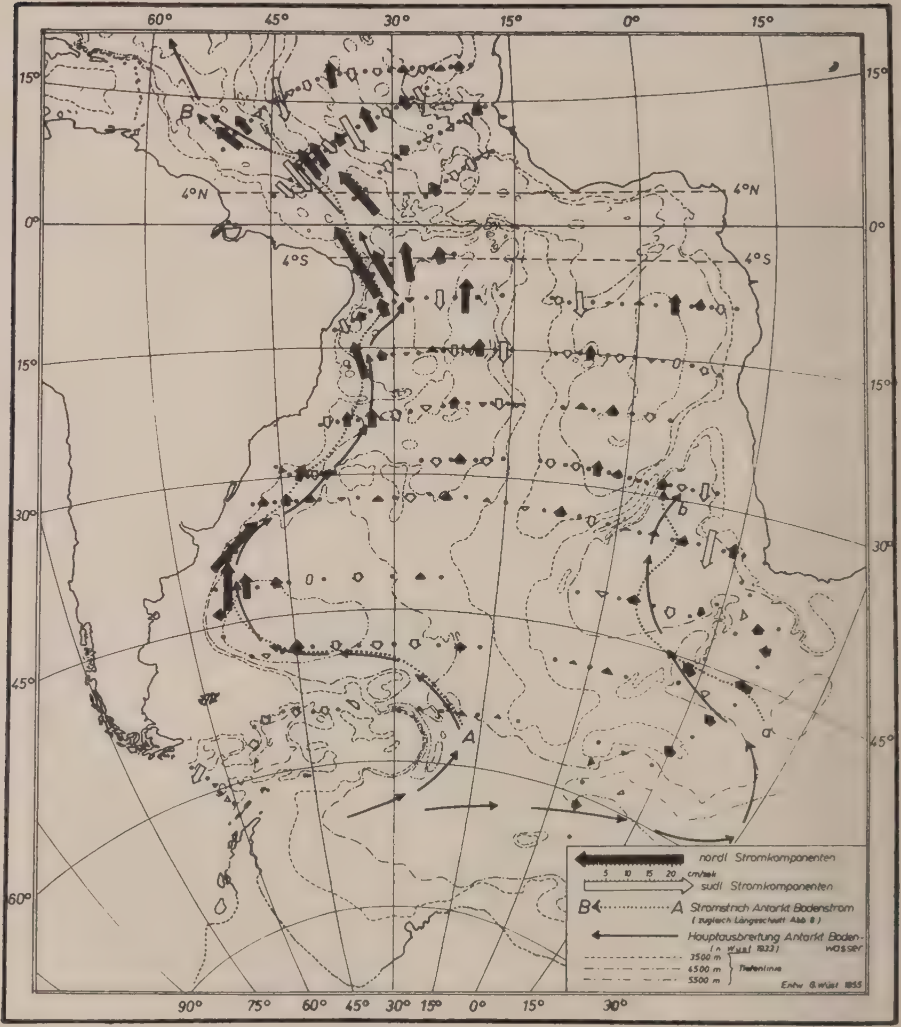


Fig. 4. Vertikalschnitt der berechneten *Geschwindigkeitskomponenten* (cm/sek) senkrecht zum "*Meteor*"—*Profil I* (Juni–Juli 1925) durch das Argentinische und das Kap-Becken in 40°–42° S.
nördliche Komponenten ausgezogene Isotacheen,
südliche Komponenten gestrichelte Isotacheen,
–O–O–O–O–dynamische Bezugsfläche n. DEFANT (1941).

von wesentlichem Einfluss auf die Wasserbewegung ist und dass die Stromlinien in den tiefsten Wasserschichten sich weitgehend den Isobathen angleichen. Die Stromkomponenten (senkrecht zu den *Meteor*- Profilen) werden sich also zumindest in der Nähe des Stromstrichs stark den Werten des wahren stationären Konvektionsstromes annähern, wobei zwar zu bedenken ist, dass sie nicht Punktwerte der

Geschwindigkeit, sondern Durchschnittswerte für einzelne Tiefenniveaus zwischen zwei benachbarten Stationen darstellen. Je weiter der Stationsabstand, umsomehr werden diese Durchschnittswerte Minimalwerte im Vergleich zu den möglichen Punktwerten der Geschwindigkeit sein, worauf wir noch zurückkommen werden. Andererseits ist zu bedenken, dass die dynamische Berechnung den Einfluss der Reibung völlig vernachlässigt. Hier hat W. HANSEN (1950) in seinen " Bemerkungen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c
90°
75°
60°
45°
30°
15°
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15°
30°
nordl Stromkomponenten
5 10 15 20 cm/sek
sudl Stromkomponenten
B A Stromstrich Antarkt Bodenstrom
(zugleich Längsschnitt Abb 8)
Hauptausbreitung Antarkt Bodenwasser
(n Wüst 1933)
3500 m
4500 m
5500 m
Tiefenlinie
Entw G. Wüst 1955

Fig. 5. Regionale Verteilung der *Geschwindigkeitskomponenten* (cm/sek) senkrecht zu den *Meteor*-Profilen (unter Weglassung der Stationen zwischen 4° N und 4° S) *in der bodennahen Schicht* der atlantischen Tiefsee (> 3500 m).*
Berechnet aus der Massenverteilung unter Zugrundelegung der von A. DEFANT (1941) abgeleiteten " dynamischen Bezugsfläche ".

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* Der Pfeil von 21 cm sek vor Kap San Roque ist zweifelhaft und zutilgen (cf. Fussnote S.386).

zu neuzeitlichen Problemen der Ozeanographie " darauf hingewiesen, dass die Berechnung der Stromgeschwindigkeiten aus dem Massenaufbau trotz der Vernachlässigung der Reibung in all *den* Fällen zu brauchbaren Resultaten führt, in denen die senkrecht zur Hauptstromrichtung existierende Druckverteilung bekannt ist und von dieser ausgegangen wird. Dies erklärt auch nach HANSEN, " warum die von WÜST (1924) durchgeführte Untersuchung des Floridastromes so gute Übereinstimmung zwischen Beobachtung und Rechnung nach dem dynamischen Verfahren trotz Vernachlässigung der Reibung lieferte." (HANSEN, 1950, S.27).* Die Orientierung der *Meteor*- Profile senkrecht zu den Isobathen der Kontinentalabfälle bietet auch aus diesem Grunde günstige Voraussetzungen für die Anwendung des BJERKNESschen Verfahrens, besonders bei der Berechnung der Stromgeschwindigkeiten in den Stromstrichen des nordatlantischen Tiefenstroms und des antarktischen Bodenstroms, die—wie wir noch zeigen werden—sich ganz an den Südamerikanischen Kontinentalabfall anlehnen.

DIE VERTIKALE VERTEILUNG DER GESCHWINDIGKEITSKOMPONENTEN IN DEN QUERSCHNITTEN

Auf Grund dieser c_1- Werte haben wir *Isotacheen-Schnitte* konstruiert, lediglich zu einer groben Veranschaulichung der Verteilung der Geschwindigkeitskomponenten senkrecht zu den Profilen und nicht etwa zur späteren Berechnung der transportierten Wassermengen, da ja eigentlich nur Punktwerte der Geschwindigkeit und nicht unsere Durchschnittswerte, die für relativ grosse Stationsabstände von 100 bis 500 km gültig sind, für eine solche Konstruktion verwendet werden dürfen. Als Beispiele reproduzieren wir hier in Fig. 3 u. 4 wieder die *Meteor*—Profile VI und I in starker Verkleinerung mit den Isotacheen für 1, 3, 5, 7 und 9 cm/sek, die im Falle nördlicher Komponenten ausgezogen, im Falle südlicher Komponenten gestrichelt sind. Wir erkennen, dass unterhalb der DEFANTschen Bezugsfläche, welche ebenfalls eingetragen ist, nur an den submarinen Steilabfällen des südamerikanischen Kontinentalblocks (und bei Profil VI auch des Atlantischen Zentralrückens) Stromgeschwindigkeiten von mehr als 3 cm/sek auftreten, dass also in der Tat im wesentlichen nur ganz auf der Westseite der atlantischen Westmulde von messbaren Geschwindigkeiten im Tiefen- und Bodenwasser gesprochen werden kann. Profil VI lehrt, dass die Strommaxima (von mehr als 9 cm/sek) im Nordatlantischen Tiefenstrom (mit südlichen Komponenten) in ca. 2250 m Tiefe etwas weiter westlich liegen als die Strommaxima (von mehr als 7 cm/sek) im antarktischen Bodenstrom (mit nördlichen Komponenten) am Tiefseeboden, d.h. der Stromstrich liegt bei diesen beiden Zirkulationsgliedern nicht in ein und derselben Vertikalfläche. Dies aber gerade ist bisher stillschweigend bei allen Bearbeitungen von Längsschnitten der Temperatur und des Salzgehalts aus der Tatsache der relativ scharfen Grenzschicht zwischen Tiefen- und Bodenwasser und der Überlagerung des Bodenwassers durch das Tiefenwasser in der ganzen Westmulde vorausgesetzt worden. Zwischen den Stationspaaren, bei denen der Stromstrich des Bodenstroms mit nördlichen Komponenten erfasst wird, existiert gar kein messbarer Tiefenstrom nach S. Bemerkenswert ist ferner, dass sowohl in Profil VI als auch in Profil I der

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* Nur im äquatorialen Bereich kann, wie auch HANSEN (1950) betont, nicht auf die Berücksichtigung der Reibung verzichtet werden, weshalb wir bei unserer Berechnung die *Meteor*-Stationen zwischen 4° N und 4° S haben wegfallen lassen.

Stromstrich des antarktischen Bodenstroms westlich der tiefsten Einsenkungen des Brasilianischen bzw. Argentinischen Beckens gelegen und um rund 1000 m auf den Kontinentalabfall heraufgeschoben ist. Bei Profil I in 41° S besitzt der nordatlantische

Tabelle I

Berechnete Stromgeschwindigkeiten und Austauschwerte im Stromstrich des Antarktischen Bodenstroms *am Westrand des Atlantischen Tiefseebodens (auf Grund dynamischer Berechnung der* Meteor-*Profile unter Benutzung der* DEFANT*schen Bezugsfläche)*

1	2	3	4	5	6	7	8	9	10	11	12
Geogr. Breite	*Meteor-Profil*	*Meteor-Stationen*		*Tiefe des Strom-maximums*	Komponenten *senkr. zum Profil*		*Wahrscheinliche Werte, auf wahre Richtung reduziert*		*Schätzung d. vertik. Austauschs*		*Bemerkungen*
	Nr.	*Nr.*	*Abstand km*	*m*	*Richtung o*	*Geschw. c_1(cm/sek)*	*Richtung o*	*Geschw c_2(cm/sek)*	*$A : c_2$ n. Defant*	*A_{-1} cm_{-1} g sec*	
10·1° N	XIII	290–289	261	5000	305	5·6	295	5·8	4	23	Nordamerikan. Becken
7·5° N	XIV	300–301	171	4500	325	7·3	295	8·4	5	42	
4·7° N	XII	260–261	158	3500	315	12·5	315	**12·5**	4	**50**	Para-Schwelle
5·3° S	IX	207–208	150	3500	330	(21·3)	330	(21·3)	2	(43)	
5·6° S	XI	251–250	309	5000	330	9·0	330	9·0	5	45	Brasilianisches Becken
10·1° S	VIII	202–201	354	5000	340	3·5	360	3·8	8	28	
16·8° S	VI	160–159	279	4500	340	7·8	340	7·8	3	23	
23·8° S	VII	167–168	315	4000	360	2·3	45	3·4	2	7*	
29·6° S	II	46– 45	210	4000	20	2·9	45	3·2	3	10	Rio-Grande Schwelle
32·7° S	IV	88– 87	276	4750	360	1·8*	45	2·6*	4	10	Argentin. Becken
37·1° S	IVa	97– 98	106	3750	50	**12·4**	50	**12·4**	3	37	
41·3° S	I	3– 4	206	5250	10	9·6	10	9·6	4	**38**	
48·5° S	III	55– 56	326	5500	360	2·1	285	7·5	(4)	29	
55·0° S	V	123–124	379	(3500)	306	(0·3)	325	(0·4)	—	—	Beobachtungen aus Bodennähe fehlen.
Mittel zw. 10° N u. 50° S				—	—	6·4	—	7·2	—	29	
Mittel zw. 10° N u. 55° S				—	—	(7·0)	—	(7·7)	—	(30)	einschl. zweifelhafte Werte

Maxima fett, Minima*, zweifelhafte Werte in ( )

Tiefenstrom keine messbaren Südkomponenten mehr; offenbar ist hier seine Energie bereits erlahmt. Die anderen, hier nicht wiedergegebenen Isotacheen-Profile (II–V, VII–XIV) zeigen ähnliche Verhältnisse, wenngleich manchmal das eine oder das andere der beiden Zirkulationsglieder weniger ausgeprägt erscheint. Aber immer zeigt sich—mit Ausnahme der südlichsten Profile V und III, wo offenbar zonale Bewegungen dominieren—auf der Westseite der westatlantischen Mulde die Intensifikation der Stromgeschwindigkeiten mit den durch diese beiden entgegengesetzten Tiefwasserbewegungen bedingten Stromkomponenten nach N bzw. S, aber in benachbarten Vertikalebenen. Auffallend ist schliesslich, dass sich der subantarktische Zwischenstrom in unseren Isotacheenprofilen nicht—auch nicht auf der Westseite—durch intermediäre Strommaxima mit messbaren Geschwindigkeiten (> 3 cm/sek) heraushebt. Offenbar werden die salzarmen subantarktischen Wassermassen noch durch die tiefreichenderen vorwiegend windbedingten Meeresströmungen der Deckschicht erfasst und bis in die tropischen Gebiete verfrachtet, und nicht durch einen eigentlichen, subantarktischen *Zwischenstrom*", der in der vertikalen Verteilung der Geschwindigkeit durch ein intermediäres Strommaximum gekennzeichnet wäre.

DIE REGIONALE VERTEILUNG DER GESCHWINDIGKEITSKOMPONENTEN IN DEN BODENNAHEN SCHICHTEN UND IM 3000-M-NIVEAU

Aus den Arbeitskarten unserer Isotacheenprofile entnehmen wir die Geschwindigkeitskomponenten c_1 der untersten, den Tiefseeboden überlagernden 250m-Schicht bei all den über 3500 m tiefen Stationspaaren und tragen sie mit Pfeilen entsprechender Länge und Richtung (positive Werte senkrecht zum Profil nach nördlichen, negative nach südlichen Richtungen) in eine Karte der Bodenströme ein (Fig. 5). Nördliche Komponenten sind durch ausgefüllte dicke Pfeile, südliche durch offene dicke Pfeile gekennzeichnet. Wir erkennen nunmehr noch klarer, dass der antarktische Bodenstrom auf der Südhalbkugel messbare Geschwindigkeiten (> 3 cm/sek) nur ganz auf der Westseite der Westmulde, d.h. am Fusse des Kontinentalabfalles etwa 1000 m über dem eigentlichen Tiefseeboden besitzt. Weiter östlich existieren—von einigen Ausnahmen besonders im Kap—und Agulhasbecken abgesehen—nur ganz schwache Komponenten. Nördlich des Äquators verlagert sich der Stromstrich des antarktischen Bodenstroms offenbar mehr nach der Ostseite der westatlantischen Mulde. Durch die punktierte Linie A — B haben wir die Strommaxima in der Westmulde (südlich des Walfischrückens auch in der Ostmulde durch die punktierte Linie a — b) verbunden und damit die Lage und Generalrichtung des Hauptstromstrichs des antarktischen Bodenstroms festgelegt. Die feinen langen Pfeile der Hauptausbreitung der Wasserart sind so genau wie möglich aus der Karte der " Ausbreitung des antarktischen Bodenwassers (dargestellt durch den prozentischen Anteil der antarktischen Komponente A_1) " übertragen, welche der Verfasser (1936, Beilage XXII) mittels der Kernschichtmethode erhalten hat. Wir stellen fest, dass sich die beiden auf unabhängige Weise gewonnenen Lagen der Achsen (Strommaxima und Hauptausbreitung des Bodenwassers) weitgehend decken. Im nördlichen Argentinischen und im Brasilianischen Becken liegt der dynamische Stromstrich um ein Stationspaar, d.h. um durchschnittlich 200 km, weiter westlich als die Achse der Ausbreitung des antarktischen Bodenwassers, was aus dynamischen Gründen zu erwarten ist. Denn

o

das Strommaximum muss mit den stärkeren horizontalen Gradienten von t und S — links von der Kaltwasserzunge der Hauptausbreitung der Wasserart—zusammenfallen. Aus dem Verlauf des Hauptstromstrichs vermögen wir nunmehr angenähert die " wahre " Richtung des Bodenstroms zwischen den betr. Stationspaaren zu erschliessen und die Geschwindigkeitskomponenten auf diese " wahren " Richtungen zu reduzieren. Dies ist in Tabelle 1 geschehen, welche in Spalte 6 und 7 die Stromkomponenten c_1 des Stromstrichs senkrecht zu den Profilen und in Spalte 8 und 9 die auf die " wahre " Richtung des Stromstrichs reduzierten Werte c_2 enthält. Wegen der günstigen Orientierung der *Meteor*-Querprofile (senkrecht zu den Steilabfällen und den vermuteten Stromrichtungen) gibt diese Reduktion beim Bodenstrom in den Geschwindigkeitswerten nur eine Vergrösserung der Geschwindigkeit um durchschnittlich 10% aus (beim Tiefenstrom von nur durchschnittlich 6%). Wir sehen aus der Tabelle, dass die einzelnen Geschwindigkeiten zwischen 2·6 cm/sek und 12·5 cm/sek variieren. Der Mittelwert aus allen Profilen zwischen 10° N und 50° S (unter Weglassung der äquatorialen Stationen zw. 4° N und 4° S) beträgt 7·2 cm/sek, ist also 4 bis 15 mal so gross wie die letzten Schätzungen von WATTENBERG (1935) und DEFANT (1936 B). *Wir haben es also im Stromstrich des antarktischen Bodenstroms in Tiefen zwischen* 3500 *und* 5500 *m mit unerwartet grossen Geschwindigkeiten zu tun,* die maximal auf 12·5 *cm/sek** ansteigen, und diese Werte stellen, wie wir noch zeigen werden, wahrscheinlich keine Höchstwerte dar. Bei einem Mittelwert von 7·2 cm/sek würden die Wassermassen im Stromstrich des antarktischen Bodenstroms 3·3 *Jahre* benötigen, um *die etwa* 7700 *km lange Strecke vom Südrand des Argentinischen Beckens* (48° S) *bis zum Nordrande des Brasilianischen Beckens* (5° *S*) zurückzulegen. Die Gesamtlänge des gewundenen Stromstrichs in der Westmulde von dem Entstehungsgebiet des antarktischen Bodenwassers in der südlichen Weddellsee (72° S) bis zum Äquator dürfte rund 12000 km betragen. Um diese Strecke *von der Antarktis bis zum Äquator* zurückzulegen, würde der Bodenstrom *rund* 5 *Jahre und* 4 *Monate* benötigen, also nur etwa den 3·4 ten Teil der Zeit von 18 Jahren, welche DEACON (1954) für den Weg des eiskalten Bodenstroms von der Antarktis zum tropischen Atlantischen als möglichen Minimalwert genannt hat. Unsere neuen Geschwindigkeitswerte gestatten uns auch, unter Benutzung der von DEFANT (1936 B) ermittelten Werte von A : c die *Beträge des vertikalen Austauschkoeffizienten A* zu schätzen; dies ist in Spalte 10 und 11 geschehen. Es ergibt sich mit 29 cm^{-1} g sec^{-1} ein *bemerkenswert hoher Mittelwert dieses Austauschkoeffizienten,* der in den einzelnen Profilen zwischen den Werten $A = 7$ und $A = 50$ schwankt. Unsere bisherigen Vorstellungen über die Grösse des Austauschkoeffizienten bedürfen also auch einer Korrektur. *Der neue Mittelwert von* $A = 29$ *ist* 7 *mal so gross als der bisher geschätzte Wert* $A = 4$; er gilt natürlich nicht für die unterste 20 — 50 m dicke Bodenwasserschicht in den Tiefseebecken, für welche es F. F. KOCZY (1950) auf Grund der *Albatross*-Messungen wahrscheinlich gemacht hat, dass sich hier die Wassermassen " anscheinend turbulenzfrei " über den Boden bewegen und der Austausch stark herabgesetzt ist. Nur an Schwellen und Bodenerhebungen ist" nach KOCZY—die Turbulenz erhöht, wodurch der Austauch beschleunigt wird.

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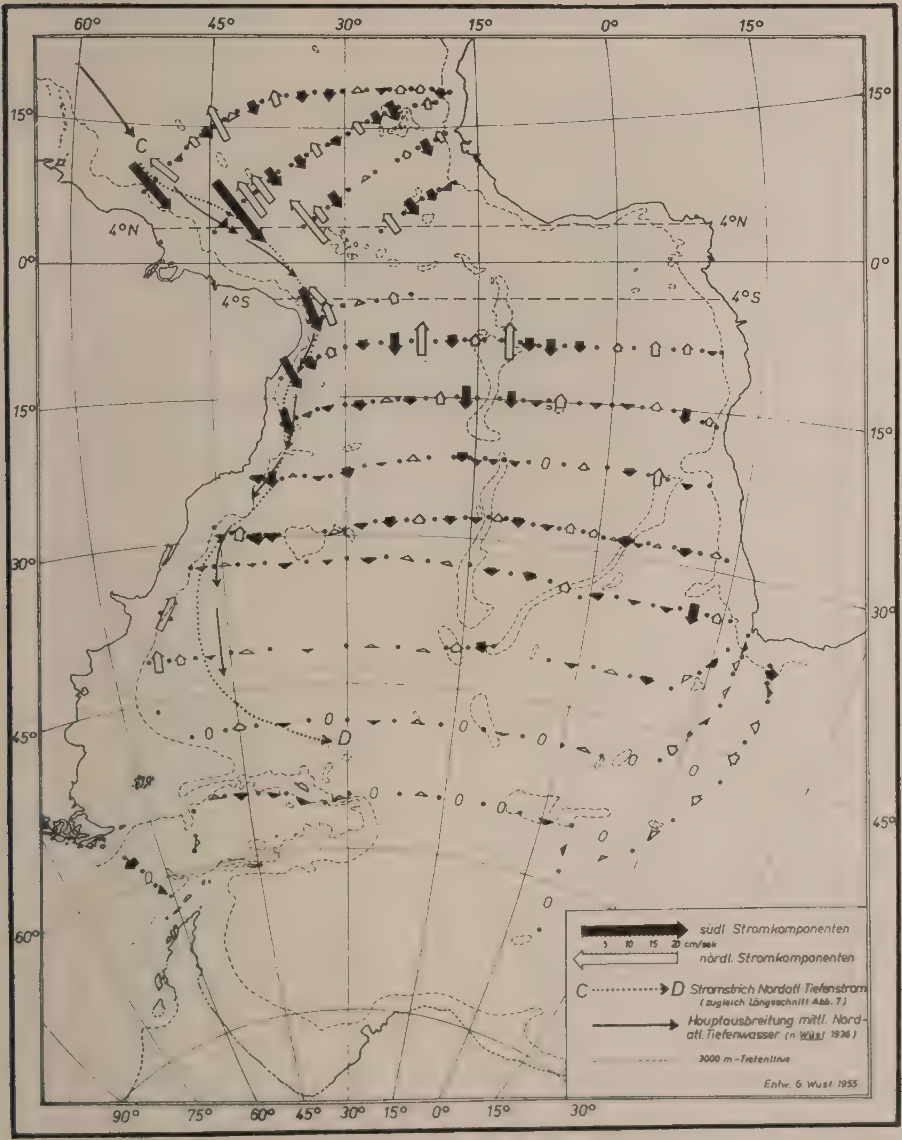
* **Zusatz bei der Korrektur:** Der für 5·3° S (Profil IX) errechnete Maximalwert von 21·3 cm sek, der noch in Fig. 5, 8 u.9 eingetragen ist, ist nachträglich als zu hoch erkannt, daher in Tab. I als zweifelhaft eingeklammert und auch im Text nicht mehr verwendet.

Eine entsprechende Tabelle mit den Stromgeschwindigkeiten und Austauschwerten haben wir aus den Vertikalschnitten auch für den *Stromstrich des Nordatlantischen Tiefenstroms,* der sich zwischen 10° N und 30° S ganz an den Westrand der westatlantischen Mulde anlehnt, zusammengestellt (Tab. II). Das Strommaximum mit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45°
60°
15°
0°
15°
30°
45°
4°N
4°N
4°S
4°S
C
D
0
90°
75°
60°
45°
30°
15°
0°
15°
30°
südl Stromkomponenten
5 10 15 20 cm/sek
nördl. Stromkomponenten
C D Stromstrich Nordatl Tiefenstrom
(zugleich Längsschnitt Abb. 7)
Hauptausbreitung mittl. Nordatl. Tiefenwasser (n. Wüst 1936)
3000 m-Tiefenlinie
Entw. G. Wüst 1955

Fig. 6. Regionale Verteilung der *Geschwindigkeitskomponenten* (cm/sek) senkrecht zu den *Meteor*-Profilen (unter Weglassung der Stationen zwischen 4° N und 4° S) *in* 3000 *m Tiefe.* Berechnet aus der Massenverteilung unter Zugrundelegung der von A. DEFANT (1941) abgeleiteten " dynamischen Bezugsfläche ".

südlichen Komponenten liegt zwischen 2000 und 3500 m Tiefe, d.h. immer in der Nähe der Kernschicht des mittleren nordatlantischen Tiefenstroms, deren Tiefenlage wir früher abgeleitet haben (WÜST 1936, Beilage XVII). Für 10° N–30° S ergibt sich

Tabelle II

Berechnete Stromgeschwindigkeiten und Austauschwerte im *Stromstrich des* Nordatlantischen Tiefenstroms *am West rand der Atlantischen Tiefsee* (*auf Grund dynamischer Berechnung der* Meteor-*Profile unter Benutzung der* DEFANT'*schen Bezugsfläche*)

1	2	3	4	5	6	7	8	9	10	11	12
Geogr. Breite	*Meteor-Profil*	*Meteor-Stationen*		*Tiefe des Strom-maximums*	Komponenten *senkr. zum Profil*		*Wahrscheinliche Werte, auf wahre Richtung reduziert*		*Schätzung d. vertik. Austauschs*		*Bemerkungen*
	Nr.	*Nr.*	*Abstand km*	*m*	*Rich-tung* o	*Ge-schw.* c_1*(cm/sek)*	*Rich-tung* o	*Ge-schw* c_2*(cm/sek)*	$A : c_2$ *n. Defant*	A_{-1} cm_{-1} *g sec*	
8·5° N	XIII	291–290	202	3000	140	11·7	110	13·6	(6)	(80)	Nordamerikan. Becken
6·2° N	XIV	299–300	259	3500	140	**17·4**	140	**17·4**	(10)	(174)	
—	XII	—	—	—	—	—	—	—	—	—	äquatoriale Zone
4·6° S	IX	208–209	167	(1800)	(150)	(6·1)	(150)	(6·1)	—	—	Berechn. reicht nur b. 2000 m
6·5° S	XI	252–251	163	3000	160	9·7	160	9·7	(6)	(40)	Brasilianisches Becken
12·3° S	VIII	204–203	259	2500	155	8·5	180	9·3	—	—	
17·6° S	VI	162–160	175	2250	165	8·4	180	8·8	—	—	
23·8° S	VII	166–167	208	3000	180	3·1	210	3·7	9	33	
29·8° S	II	45– 44	172	3250	180	1·8	210	2·1*	10	21	
32·5° S	IV	89– 88	271	3000	180	(0·6*)	(180)	(0·6)	—	—	Argentinisches Becken
41·6° S	I	5– 6	372	3250	(180)	(0·2)	(180)	(0·2*)	—	—	
48·5° S	III	55– 56	326	2000	(180)	(0·4)	(150)	(0·5)	—	—	
Mittel zw. 10° N und 30° S					—	8·7	—	9·2	—	27	(ohne den eingeklamm. Wert)
Mittel zw. 10° N und 50° S					—	(6·2)	—	(6·5)	—	(70)	incl. eingeklammerte Werte.

Maxima fett, Minima*, zweifelhafte Werte in ( )

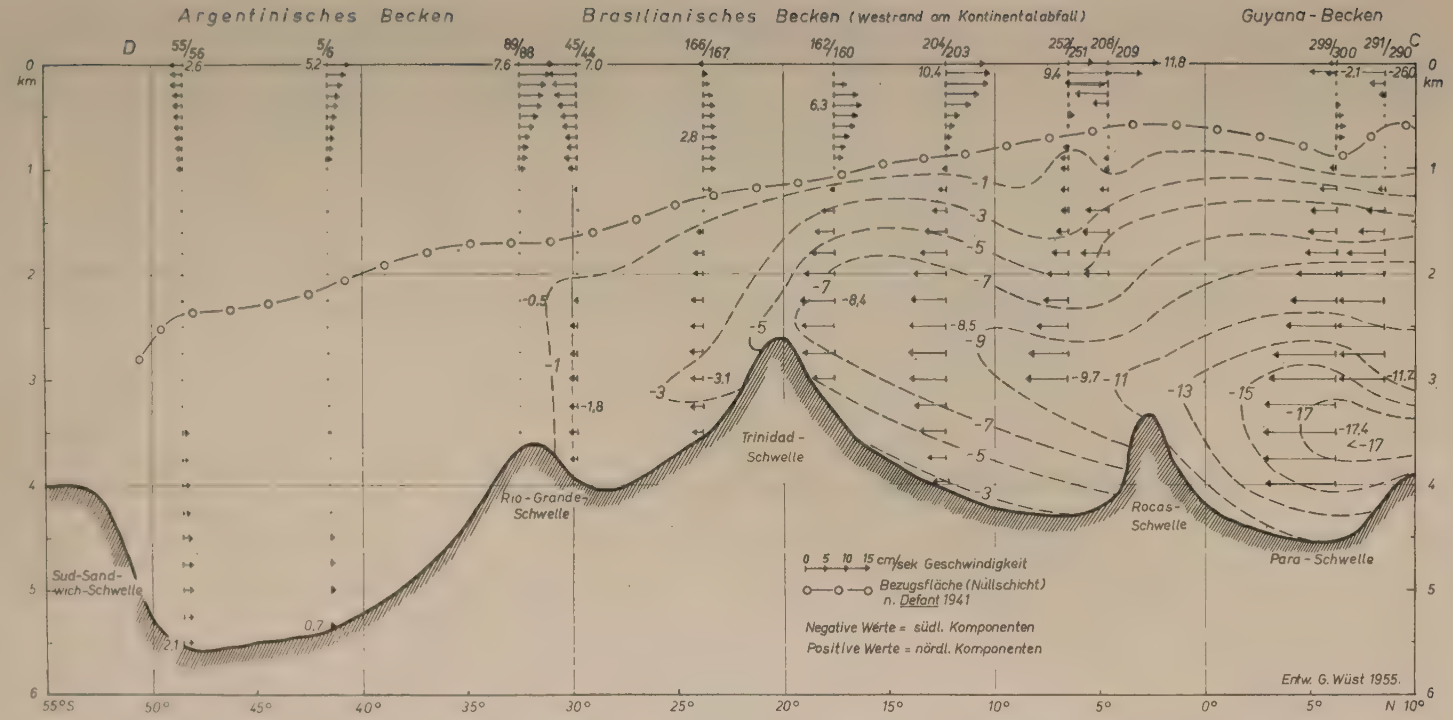

Fig. 7. *Längsschnitt der Geschwindigkeit* (cm/sek) der Stromkomponenten (senkrecht zu den *Meteor*-Profilen) *im Stromstrich* D – C (vgl. Fig. 6) *des Nordatlantischen Tiefenstroms* am Westrand der Atlantischen Tiefsee (auf Grund dynamischer Berechnung der *Meteor*-Profile).

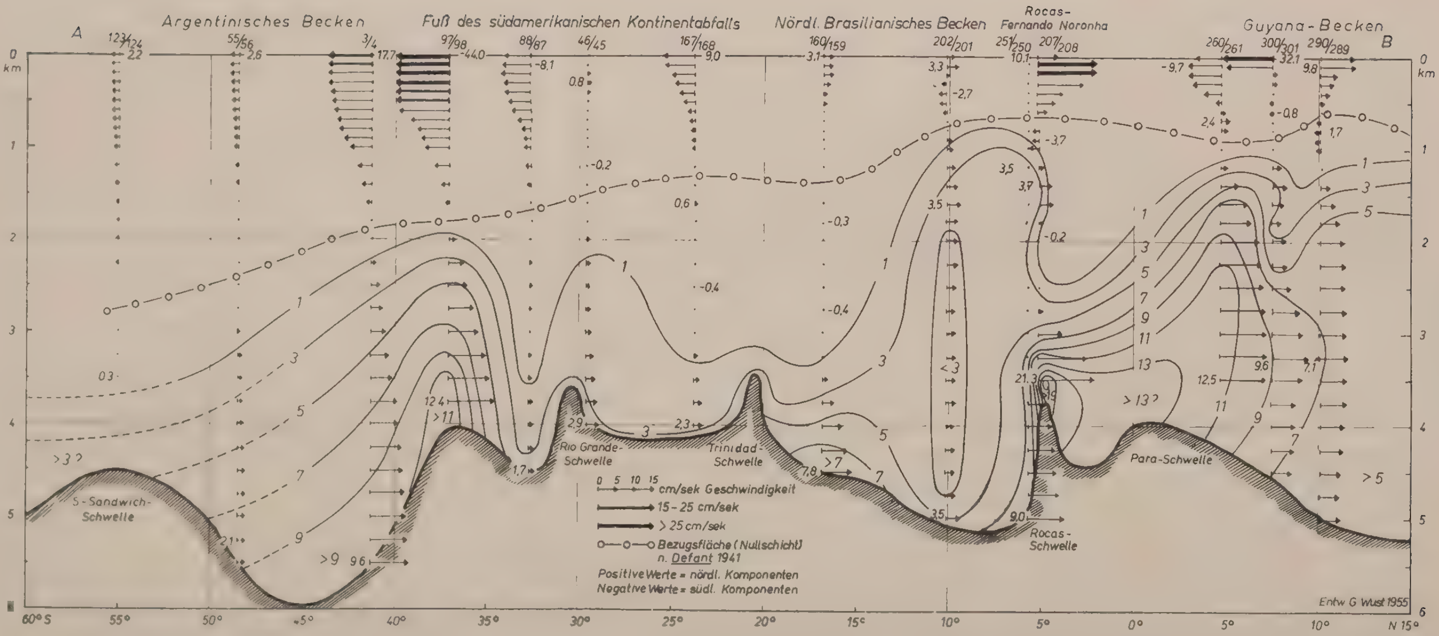

Fig. 8. *Längsschnitt der Geschwindigkeit* (cm/sek) der Stromkomponenten (senkrecht zu den *Meteor*- Profilen) *im Stromstrich A – B* (vgl. Fig. 5) *des Antarktischen Bodenstroms* am Westrand der Atlantischen Tiefsee (auf Grund dynamischer Berechnung der *Meteor*-Profile).*

* Betreff. des zweifelhelhaften Wertes von 21·3 cm/sek in 3500 m (cf. Fussnote S.386).

im Stromstrich als Mittelwert der Komponenten (senkrecht zum Schnitt) ein Wert von 8·7 cm/sek, bei Reduktion auf die " wahre " Richtung von 9·2 cm/sek; die Einzelwerte schwanken zwischen 1·8 (bzw. 2·1) und 17·4 cm/sek. Diese Werte liegen etwas höher als die Werte, die DEFANT (1941) für 2000 m Tiefe, d.h. etwa für die Schicht des *oberen* nordatlantischen Tiefenwassers, erhalten hat. Die Schätzung des vertikalen Austauschkoeffizienten, der sich im Mittel zu $A = 27$ cm^{-1} g sec^{-1} ergibt, ist hier mit grösseren Unsicherheiten behaftet, da für diese Schichten nur spärlichere Angaben des Wertes $A : c$ seitens DEFANT vorliegen.

Da das Strommaximum des Tiefenstroms mit südlichen Komponenten im Mittel etwa bei 3000 m Tiefe liegt, wählen wir dieses Niveau von 3000 m, um die regionale Verteilung der Geschwindigkeitskomponenten in der Nähe der Kernschicht des mittleren Nordatlantischen Tiefenwassers kartographisch darzustellen (Fig. 6). Wir erkennen, dass sich zwischen 10° N und 30° S der Stromstrich des Tiefenstroms —in noch stärkerem Masse als der Bodenstrom—ganz an den südamerikanischen Kontinentalabfall anlehnt und dass weiter östlich und südlich kaum noch messbare Geschwindigkeiten auftreten. Nur dort, wo der antarktische Bodenstrom eine grosse vertikale Mächtigkeit besitzt, treten in unserer Karte von 3000 m messbare nördliche Geschwindigkeitskomponenten auf (offene Pfeile). Die punktierte Linie C — D stellt den Hauptstromstrich des Tiefenstroms dar und ist gegeben durch die Verbindungslinie der Strommaxima. Südlich 30° S ist diese Linie hypothetisch, da hier die meridionalen Komponenten unter die Grenze der Messbarkeit (3 cm/sek) sinken. Dieser Hauptstromstrich *C — D* des nordatlantischen Tiefenstroms deckt sich, wie unsere Karte lehrt, weitgehend mit der Achse der Hauptausbreitung des mittleren nordatlantischen Tiefenwassers, die wir 1936 aus der Kernschicht des intermediären Sauerstoffmaximums erschlossen haben (WÜST, 1936, Beilage XVIII) —wiederum ein Beleg für die innere Übereinstimmung der Ergebnisse der beiden Methoden, des dynamischen Verfahrens und der Kernschichtmethode.

DIE LÄNGSSCHNITTE DER GESCHWINDIGKEIT IN DEN STROMSTRICHEN

Das neue Bild, das wir durch die dynamische Bearbeitung der *Meteor*-Profile von den Stromvorgängen in der atlantischen Tiefsee zwischen 10° N und 55° S gewonnen haben, wollen wir abrunden durch die Konstruktion von Längsschnitten der Geschwindigkeit längs den Stromstrichen des nordatlantischen Tiefenstroms und des antarktischen Bodenstroms am Westrande der Westmulde (Figs. 7 und 8). Die Lage der beiden Längsschnitte *C — D* und *B — A* ergibt sich aus den beiden Karten der Geschwindigkeitskomponenten (Figs. 5 und 6). Durch Vergleich dieser beiden gewundenen Linien erkennen wir, dass die vertikale Schnittfläche, d.h. der Stromstrich des nordatlantischen Tiefenstroms zwischen 10° N und 35° S um durchschnittlich 200 km westlicher liegt als Schnittfläche und Stromstrich des antarktischen Bodenstroms. Im Argentinischen Becken zwischen 35° S und 50° S ist das Umgekehrte der Fall.

Der *Geschwindigkeitslängsschnitt des Nordatlantischen Tiefenstroms* (Fig. 7) zeigt zwischen 10° N und 33° S ein in sich geschlossenes und durchaus plausibles Isotacheenbild. Das von N nach S kontinuierlich abnehmende Strommaximum liegt allenthalben 300–700 m, im Durchschnitt 500 m über dem zwischen 2500–4500 m Tiefe gelegenen Meeresboden. Der Tiefenstrom reicht in diesen Breiten überall bis zum Meeresboden; er wird nicht von nördlichen Komponenten eines Bodenstroms unterlagert. Nur südlich 40° S tritt der Bodenstrom schwach in Erscheinung.

Der nordatlantische Tiefenstrom mit seinen meridionalen Komponenten endet praktisch bereits in 33° S. Die Maximalwerte der Stromgeschwindigkeit nehmen in gesetzmässiger Weise von 17·4 cm/sek in 6·2° N (über der Para-Schwelle) bis auf 1·8 cm/sek in 29·8° S (über der Rio-Grande-Schwelle) ab. Diese Abnahme der maximalen Stromgeschwindigkeit nach S scheint nicht streng proportional mit der zurückgelegten Entfernung zu erfolgen, sondern im Bereich der Schwellen (Para-Schwelle, Trinidad-Schwelle) rascher vor sich zu gehen. Der Tiefenstrom reicht nach oben bis zur Bezugsfläche, die nach DEFANT (1941) von 600 m in 10° N auf 1700 m in 33° S abfällt. In den Zonen zwischen 10° N und 33° S wird innerhalb unserer Schnittfläche der ganze Raum zwischen Bezugsfläche und Meeresboden vom Tiefenstrom mit südlichen Komponenten eingenommen. Dieses Strombild steht in guter innerer Übereinstimmung mit der Ausbreitung des sauerstoffreichen Tiefenwassers (> 5 ccm), wie wir sie in dem ganz auf der Westseite gelegenen Hauptschnitt dargestellt haben (WÜST, 1936, Beilage XXIII). Auch hier endet diese Ausbreitung in ca. 35° S.

Der *Geschwindigkeits-Längsschnitt des antarktischen Bodenstroms* (Fig. 8) zeigt nicht ein so geschlossenes Strombild. Das Strommaximum liegt mit variierenden Werten zwischen 2 und 13 cm/sek allenthalben in Bodennähe. Nur zwischen 5° N und 10° N, d.h. im Guyana-Becken, befindet es sich, nachdem der Bodenstrom die Para-Schwelle überschritten hat, merklich über dem Tiefseeboden, Die bodennahen Geschwindigkeitsmaxima nehmen nicht in gesetzmässiger Weise von S nach N, d.h. in der Richtung des Bodenstroms ab. In dieser um 200 km gegenüber dem Stromstrich des Tiefenstroms seitlich nach E verschobenen Schnittfläche wird vielfach der ganze Raum zwischen Bezugsfläche und Tiefseeboden von Nordstrom eingenommen. Nur im Brasilianischen Becken zeigt er mehrfach eine geringere vertikale Mächtigkeit und gibt darüber schwachen südlichen Komponenten Raum. Auffallend sind die isolierten Strommaxima von mehr als 12 cm/sek in 37° S und von mehr als 13 cm/sek in ca.5° S, die mit der Morphologie in Zusammenhang zu stehen scheinen. Auf jeden Fall sind im Isotacheenbild des antarktischen Bodenstroms die grossen Gesetzmässigkeiten, wie wir sie 1933 aus den Längsschnitten der potentiellen Temperatur ablesen zu können meinten, durch eine Reihe von Zufälligkeiten, die sicher z.T. in den Fehlerquellen des dynamischen Verfahrens liegen, überdeckt. Bodenstrom und Tiefenstrom sind offenbar nicht Glieder *einer* in sich geschlossenen meridionalen Zirkulation innerhalb ein und derselben vertikalen Schnittfläche, sondern sind nebeneinander gelagert am schräg zur Tiefsee einfallenden Kontinentalabfall, so dass der nordatlantische Tiefenstrom den antarktischen Bodenstrom verdrängt und selbst bis zum Boden mit südlichen Komponenten reicht und umgekehrt. So sind die schematischen Auffassungen, die wir 1936 aus den Länsgschnitten der ozeanographischen Faktoren und mittels der Kernschichtmethode gewonnen haben, in dieser Hinsicht zu modifizieren. *Wasserartgrenzen können nicht*—auch nicht, wenn sie so ausgeprägt sind wie in der Westmulde zwischen dem Bodenwasser und dem Tiefenwasser—*identisch sein mit Zirkulationsgrenzen.* In unseren Längsschnitten der Geschwindigkeiten haben wir durch Pfeile die Stärke der meridionalen Komponenten des stationären Gradientstroms auch in den oberhalb der Bezugsfläche gelegenen Schichten dargestellt. *Es ist ersichtlich, dass die Stromgeschwindigkeiten in den grossen Tiefen und in Bodennähe in den Stromstrichen grössenordnungsmässig gelegentlich den Geschwindigkeiten der Konvektionsströmungen in den oberflächlichen*

Schichten nahekommen—eine Konsequenz, die auf den ersten Blick überraschen muss, da sie zu den im Grunde noch immer vorherrschenden Vorstellungen kaum messbarer Wasserbewegungen in der Tiefsee (siehe DEACON 1954) im Widerspruch steht.

KRITIK DER ERGEBNISSE

Unsere Ergebnisse über die absoluten Stromgeschwindigkeiten in der Tiefsee stehen und fallen mit den Annahmen über die Tiefenlage der " dynamischen Bezugsfläche ", in denen wir uns ganz an DEFANTS Auffassungen (1941) angeschlossen haben. So lange nicht die praktische Brauchbarkeit der Annahmen über diese in sich geschlossene gekrümmte " Nullschicht " auf andere Weise—etwa durch systematische Strommessungen in den grossen Tiefen (was bisher nicht möglich gewesen ist) —erwiesen ist, kann *unsere Untersuchung nur als ein neuer Versuch* gewertet werden, in dieser wichtigen Frage der absoluten Tiefwasserbewegungen einen Schritt weiterzukommen. Die innere Übereinstimmung der abgeleiteten Stromfelder in sich und mit den durch die Kernschichtmethode gewonnenen Vorstellungen scheint—wie auch bei der Untersuchung von DEFANT (1941)—dafür zu sprechen, dass mit unseren Versuchen zunächst eine *geophysikalisch sinnvolle*, *erste Approximation* an die Wirklichkeit gefunden ist. Jedoch müssen wir uns im klaren sein, dass selbst dann, wenn die DEFANTsche Bezugsfläche sich als richtig erweisen sollte, unsere Geschwindigkeitswerte auch *nur grobe Annäherungen* darstellen können wegen der verschiedenen, schwer abschätzbaren weiteren Fehlerquellen des dynamischen Verfahrens, die sich aus der Vernachlässigung der Reibung, der Annahme stationärer Bedingungen und der Weitabständigkeit der Stationen ergeben.

Dass die aus der Vernachlässigung der Reibung resultierende Fehlerquelle in all den Fällen bedeutungslos ist, wo die Strömungen praktisch senkrecht zu den *Meteor*-Profilen verlaufen, d.h. besonders in den Stromstrichen am südamerikanischen Steilabfall, haben wir schon oben betont. Aber zweifellos kann durch diese Fehlerquelle in den übrigen Gebieten die Vergleichbarkeit der berechneten Stromkomponenten herabgesetzt sein. Auch die Annahme stationärer Bedingungen kann vielfach nur in grober Annäherung erfüllt sein, wenn wir mit A. DEFANT (1950) an die Wirkungen der internen Wellen (von Gezeitenperiode) auf den vertikalen Massenaufbau denken und an die Verfälschungen, die hierdurch bei den dynamischen Berechnungen auftreten können. Auf die Möglichkeit solcher Verfälschungen war der Verfasser schon während der *Meteor*-Expedition aufmerksam geworden, als " die systematische Untersuchung der periodischen Schwankungen von Temperatur und Salzgehalt auf den Ankerstationen ergeben hatte, dass die einmalige Durchführung der obersten 200 m tief reichenden Serie zur Erfassung des mittleren Zustandes nicht ausreicht ". "Aus diesem Grunde wurden auf den Profilen VIII, IX und X während der Stationsaufenthalte regelmässige dreistündige Wiederholungen der obersten Serie vorgenommen ", gelegentlich bis 1000 m Tiefe (WÜST, 1932, S.37/38). In diesen Profilen beruhen also unsere dynamischen Berechnungen in den oberen Serien auf *mittleren* Zustandskurven, wodurch der Einfluss interner Wellen weitgehend ausgeschaltet ist. In allen anderen Profilen müssen wir damit rechnen, dass die Anzahl der Solenoide zwischen den Stationspaaren durch die Wirkungen interner Wellen mehr oder minder verfälscht sein kann.

Schliesslich haben wir schon betont, dass *bei dem relativ weiten Stationsabstand die von uns berechneten Schichtmittelwerte der Stromgeschwindigkeit nur Minimalwerte* sein können im Vergleich zu den möglichen Punktwerten der Geschwindigkeit, wie sie etwa durch direkte Strommessungen erhalten werden. Alle feineren Züge der Zirkulation müssen durch diese Art der Berechnung und Mittelbildung abgeschwächt bzw. ausgetilgt werden, worauf STOMMEL (1949, S.214) in seinen ausgezeichneten Betrachtungen über " The Necessity of a Spectrum of Eddies in the Ocean " hingewiesen hat. Die Existenz eines ganzen Spektrums von den grossen Wirbeln der grossen Meeresströmungen über die kleineren Wirbel bis zu den kleinsten molekularen Wirbeln herab, ist also nach ihm notwendig für den Verbrauch der kinetischen Energie, welche durch die Tangentialkraft des Windes auf die Meeresoberfläche übertragen wird. Alle Spitzenwerte der Geschwindigkeit werden auf diese Weise reduziert, alle Kompenenten der Wasserbewegung, die zu einer niedrigeren Ordnung der ganzen Skala gehören, müssen in den Ergebnissen so " weitabständiger " Berechnungen fehlen. " Therefore, it is important to recognize that the term " velocity " is meaningless unless accompanied by some indication of the mode of averaging employed in its determination." (STOMMEL 1949, S.215). Wesentlich wäre nun, dass, um wenigstens die regionale Vergleichbarkeit der berechneten Geschwindigkeiten sicherzustellen, die Stationspaare jeweils ungefähr denselben Abstand besässen. Der mittlere Stationsabstand auf den *Meteor*-Profilen dürfte bei 200–300 km liegen, im einzelnen aber variieren die Abstände zwischen rund 100 und rund 500 km mit einer Verdichtung über den Steilabfällen. Das muss zur Folge haben, dass unsere neuen Geschwindigkeitswerte in den Tabellen, Karten und Schnitten nicht streng vergleichbar sind und dass eine Reihe der regionalen Unterschiede, wie z.B. in dem Geschwindigkeitslängsschnitt für den Stromstrich des antarktischen Bodenstroms, auf "Zufälligkeiten" in den Stationsabständen beruhen. Darauf deutet auch Fig. 9, in welche die für den Stromstrich des Bodenstroms berechneten Geschwindigkeiten in Beziehung gesetzt sind zu den korrespondierenden Stationsabständen.

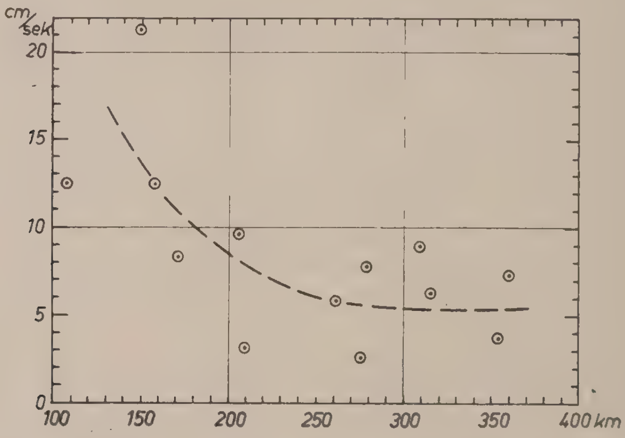

Fig. 9. Beziehung zwischen den berechneten Stromgeschwindigkeiten in cm/sek (im Stromstrich des Antarktischen Bodenstroms) und den zugehörigen Stationsabständen in km.

Bei aller Streuung der Punkte ist eine Abhängigkeit unverkennbar: bei Abständen von 100–160 km liegen die Geschwindigkeitswerte zwischen 12 und (21)* cm/sek, bei Abständen von 200–360 km liegen die Werte zwischen 2 und 10 cm/sek. Hieraus können wir folgern, dass wir allenthalben im Stromstrich des antarktischen Bodenstroms Geschwindigkeiten von mehr als 10 cm/sek gefunden haben würden, wenn der Stationsabstand grundsätzlich überall 100 km betragen hätte. Das grosse Programm der systematischen Aufnahme eines ganzen Ozeanraumes innerhalb 2 1/4 Jahre hat damals bei der *Meteor* Expedition eine solche Verdichtung des Stationsnetzes nicht gestattet. MERZ hat damals auf die Erfassung von kleineren Grenzwirbeln, solcher 2. Ordnung, verzichtet, " die späterhin Aufgaben für oft wiederholte Spezialuntersuchungen abgeben könnten " (1925, S.575) und sich für grössere Stationsabstände von ca. 2½ Längengraden entschieden, die er für die Erfassung der " grossen stationären Wirbelbildungen, deren Kenntnis für eine tiefere Erkenntnis der Bewegungsvorgänge unentbehrlich erscheint ", erforderlich gehalten hat. Bewusst ist also MERZ hinter den Auffassungen (besonders norwegischer Forscher) zurückgeblieben, die für die dynamische Berechnung der Meeresströmungen einen wesentlich kleineren Stationsabstand—damals 20 sm, heute 10 sm—gefordert haben. Bei der Bearbeitung des Bimini-Schnittes, bei dem der Abstand der Stationsvertikalen mit 16 km immer unter 10 sm geblieben ist, hat der Verfasser (WÜST 1924, S.35–41) unter Benutzung der aus Strommessungen und dem vertikalen Aufbau erschlossenen Nullfläche zeigen können, dass hier im Floridastrom die aus dem Massenfeld berechneten Schichtmittelwerte der Geschwindigkeit ganz im Einklang stehen mit den von PILLSBURY (1891) direkt gemessenen Punktwerten der Geschwindigkeit. Aus all diesen Überlegungen müssen wir folgern, dass im Stromstrich des Tiefenstroms bzw. des Bodenstroms die Spitzenwerte der berechneten Geschwindigkeiten noch höhere Beiträge als 17 bzw. 13 cm/sek erreichen könnten, wenn die Stationsabstände nur 20–40 km gross gewesen wären. Damit gewinnt unsere frühere Behauptung *noch mehr an Wahrscheinlichkeit, dass die Stromgeschwindigkeiten in der Tiefsee in den Stromstrichen an den Kontinentalabfällen grössenordnungsmässig gelegentlich den Geschwindigkeiten der Konvektionsströmungen in den oberflächlichen Schichten nahekommen*—wenn man dabei natürlich von den extremen Geschwindigkeiten im Golfstromsystem oder in ähnlich starken Gefällsströmungen absieht. Aber diese Behauptung gilt nur in dem Masse, in dem sich die DEFANTschen Annahmen über die Tiefenlage der dynamischen Bezugsfläche als brauchbare Annäherungen erweisen, was heute nur aus verschiedenen Indizien vermutet, aber nicht bewiesen werden kann. Die Bewegungsgrösse ist der nach Raum und Zeit variabelste ozeanographische Faktor, und nichts kann die heutige Lage der dynamischen Ozeanographie—auch im Hinblick auf die Tiefenzirkulation—besser charakterisieren als die folgenden Worte STOMMELS (1949, S.224): In fact, there seems to be no means of achieving a sharply focused picture in the study of ocean currents. What appeared yesterday as a smooth broad stream appears today as an amazingly corrugated irregular one, and tomorrow probably ever finer details of greater complexity will make an appearance. So the oceanographer is assailed by growing doubts as to whether or not he can ever hope to describe the details with any meaning." Eine solche Skepsis darf uns aber natürlich nicht hindern, zu versuchen, das Problem der Geschwindigkeit der Tiefwasserbewegungen mit allen nur denkbaren quantitativen Methoden weiterhin in Angriff zu nehmen und zu immer grösseren Annäherungen an die Wirklichkeit zu gelangen. Hier möchte ich auf das ideenreiche, vielfach fast philosophisch anmutende Buch von H. B. Bigelow (1931) hinweisen, betitelt “ Oceanography, its scope, problems and economic importance ”, wo er in dem noch heute sehr lesenswerten Abschnitt über die Zirkulationsprobleme schreibt: “ In this field, the task immediately urgent is to determine, for as many sectors of different currents as possible, and for as many different ocean areas, whether the internal hydrostatic forces at work are, or are not, quantitatively sufficient, and do, or do not, act in the direction proper to produce the general type and velocity of circulation that other lines of evidence have shown to prevail ”. Die vorliegende Untersuchung, die später an anderer Stelle durch die Berechnung der durch die *Meteor*-Profile transportierten Wassermengen fortgeführt wird, versucht, hinsichtlich der Tiefen- und Bodenströmungen in der atlantischen Tiefsee einen Beitrag zur Beantwortung dieser Fragen Bigelows zu liefern.*

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* Dieser Wert ist zu hoch (cf. Fussnote S.386).

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* Wir haben es bisher vermieden, von den Ursachen dieser Tiefenzirkulation zu sprechen, zumal es sich ja hierbei um Kreisprozesse handelt. Letzten Endes steht natürlich die Asymmetrie der atlantischen, über den Äquator nach beiden Seiten weit hinausgreifenden Tiefwasserbewegungen in Zusammenhang mit der zum Äquator asymmetrischen Verteilung von Wasser und Land auf Nord- und Südhemisphäre, den stärkeren kontinentalen Einflüssen im N, den seitlichen Begrenzungen des “ atlantischen Tales ” und der Existenz von Nebenmeeren in seiner Nordhälfte. In dieser Frage sei auf das Referat eines Vortrags von E. T. Eady über “ Circulation of waters in the oceans ” (*Nature*, April 1951, S.513–515) verwiesen, in welchem sich folgende interessanten Ausführungen finden: “ Regarding the causes of this circulation, Dr. Eady hazarded the guess that the difference in ocean geography between the hemispheres is responsible. The wind-stress in the Roaring Forties‘ ’ must generate a vertical circulation which in the absence of land barriers would cause descent near 30° S. But the Atlantic, unlike the Antarctic, is bounded laterally, and it seems possible that the water follows the path of least resistance, flowing up to high latitudes where its high density enables it to be easily forced down. (The existence of a land boundary is necessary to enable the water to adjust its angular momentum, through external pressure, during its change of latitude).” Leider hat Eady, soweit dem Verfasser bekannt ist, diese Untersuchungen über die Tiefenzirkulation bisher nicht in extenso veröffentlicht.

REFERENCES

Bigelow, H. B. (1931), *Oceanography, its Scope, Problems and Economic Importance*. London, Chapman and Hall, 263 pp.

Bowden, K. F. (1954), The direct measurement of subsurface currents in the ocean. *Deep-Sea Res.*, **2** (1), 33–47.

Castens, G. (1931), Stromgeschwindigkeiten und Wasserumsätze in den Tiefen des Ozeans. *Ann. Hydrogr.*, usw., **59**, 335–339.

Castens, G. (1932), Tiefenstrom-Geschwindigkeiten im Nordatlantischen Ozean. *Ann. Hydrogr.*, usw., **60**, 39–41.

Deacon, G. E. R. (1931), Velocity of deep currents in the South Atlantic. *Nature*, **128**, 267.

Deacon, G. E. R. (1954), Exploration of the deep sea. *J. Inst. Navig.*, **7** (2), 165–174.

Defant, A. (1935), Zur Dynamik des antarktischen Bodenstromes im Atlantischen Ozean. *Z. Geophys.*, **11**, 50–55.

Defant, A. (1936 a), Die Troposphäre. *Wiss. Ergeb. Deutsch. Atlant. Exped.—“ Meteor ”*, **6** (1, 3), 289–411.

Defant, A. (1936 b), Ausbreitungs- und Vermischungsvorgänge im Antarktischen Bodenstrom und im subantarktischen Zwischenwasser. *Wiss. Ergeb. Deutsch. Atlant. Exped.—“ Meteor ”*, **6** (2, 2), 55–96.

efant, A. (1941), Die absolute Topographie des physikalischen Meeresniveaus und die Druckflächen, sowie die Wasserbewegung im Atlantischen Ozean. *Wiss. Ergeb. Deutsch. Atlant. Exped.—“ Meteor ”*, 1925–1927, **6** (2, 5), 191–260.

Defant, A. (1950), Reality and illusion in oceanographic surveys. *J. Mar. Res.* **9** (2), 120–138.

Forch, C. (1911), *Kaysers Physik des Meeres*. Paderborn, 377 pp.

Hansen, W. (1950), Bemerkungen zu neuzeitlichen Problemen der Ozeanographie. *Dtsch. Hydrogr. Z.*, **3** (1/2), 20–23.

Helland-Hansen, B. (1934), The Sognefjord section. In: *James Johnstone Memorial Volume*, Liverpool Univ. Press, 257–274.

Koczy, F. F. (1950), Die bodennahen Wasserschichten der Tiefsee. *Naturwissenschaften*, **37** (15), 360.

Merz, A. (1925), Die Deutsche Atlantische Expedition auf dem Vermessungs- und Forschungensschiff *Meteor*. *Sitzungsber. Preuss. Akad. Wissenschaft, Berlin*, Phys.-Math. Kl., **31**, 562–586.

Mosby, H. (1934), The waters of the Atlantic Antarctic Ocean. *Sci. Res. Norwegian Antarctic Exped.*, 1927–1928, **1** (11), 1–131.

Pillsbury, J. E. (1891), The Gulf Stream. A description of the methods employed in the investigations and the results of the research. *Rept. Superintendent, U.S. Coast and Geodetic Survey, Appendix* **16**,

Riley, G. A. (1951), Oxygen, phosphate and nitrate in the Atlantic Ocean. *Bull. Bingham Oceanogr. Coll.*, **13** (1), 1–126.

Seiwell, H. R. (1934), The distribution of oxygen in the western basin of the North Atlantic. *Pap. Phys. Oceanogr., Meteorol.*, **3** (1), 1–86.

Stommel, H. (1949), Horizontal diffusion due to oceanic turbulence. *J. Mar. Res.*, **8** (3), 199–225.

Thoulet, J. (1921), Sur la circulation océanique profonde. *Bull. Inst. Océan., Monaco*, **404**, 1–10.

Thoulet, J. (1925), Contribution à l'étude de la circulation océanique. *Ann. Inst. Océanogr., Monaco*, **2**, 409–423.

Wattenberg, H. (1927), Dritter Bericht über die chemischen Arbeiten. *Z. Gesellschaft Erdkunde, Berlin*, **3**, 137–143.

Wattenberg, H. (1935), Kalkauflösung und Wasserbewegung am Meeresboden. *Ann. Hydrogr.*, usw., **63**, 387–391.

Worthington, L. V. (1954), A preliminary note on the time scale in the North Atlantic circulation. *Deep-Sea Res.*, **1**, 244–251.

Wüst, G. (1924), Florida- und Antillenstrom. Eine hydrodynamische Untersuchung. *Veröff. Inst. Meereskunde, Berlin*, **12**, 1–48.

Wüst, G. u.a. (1932), Ozeanographische Instrumente und Methoden. Das ozeanographische Beobachtungsmaterial. *Wiss. Ergeb. Deutsch. Atlant. Exped.—" Meteor "*, 1925–1927, 4 (1/2), 1–298.

Wüst, G. (1933), Das Bodenwasser und die Gliederung der Atlantischen Tiefsee. *Wiss. Ergeb. Deutsch. Atlant. Exped.—" Meteor "*, 1925–1927, **6** (1, 1), 1–107.

Wüst, G. (1935), Die Stratosphäre. *Wiss. Ergeb. Deutsch. Atlant. Exped.—" Meteor "*, 1925–1927, **6**, (1, 2, Atlas), 109–288.

Wüst, G. (1938 a), Die dynamischen Werte für die Standardhorizonte an den Beobachtungsstationen. *Wiss. Ergeb. Deutsch. Atlant. Exped.—" Meteor "*, 1925–1927, **6** (2, 3), 99–181.

Wüst, G. (1938 b), Bodentemperatur und Bodenstrom in der atlantischen, indischen und pazifischen Tiefsee. *Gerlands Beiträge zur Geophysik*, **54** (1), 1–8.

Wüst, G. (1951), Über die Fernwirkungen antarktischer und nordatlantischer Wassermassen in den Tiefen des Weltmeeres. *Naturwiss. Rundschau*, **3**, 97–108.

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U.S. participation in conservation of international fishery resources

By WM. C. HERRINGTON

IN THE Fourth International Fishery Congress held in Washington, D.C., in 1908, Mr. CHARLES E. FRYER, Superintending Inspector of the Board of Agriculture and Fisheries of the United Kingdom, made the following statement: " The further afield the fishermen of any state go, the more certainly will they be brought into closer relations with the fishermen of fresh nationalities, and the longer will be the list of states which find that they have interests in common—interests which will, sooner or later, call for combined action in the direction of international regulations of the fisheries on the high seas."

Time has proven Mr. FRYER a most competent prophet. With the passing years and development of more efficient and intensive fishing activities, the international problems and frictions arising from fishing activities have multiplied. Numerous attempts have been made to find solutions to these problems through international agreements. Many of the most extensive and successful of these attempts have been in the Western Hemisphere.

Here, beginning some forty years ago, the United States and Canada working together, and in more recent years with other countries, have embarked on a system of fishery conservation conventions which are proving successful in restoring and safeguarding the productivity of common high-seas fishery resources. Progress has been made through careful step-by-step exploration and development. This exploration has been directed first towards developing and co-ordinating research, and secondly, after research demonstrated the necessity, towards devising practical and effective conservation measures to ensure the maximum sustainable productivity of the particular fishery. As one step proved itself, and convinced an always sceptical fishing industry and public, which watched with a critical eye this increasing delegation of responsibility and authority to an international body, it was possible to move on to development and adoption of additional measures to handle more difficult, involved, or controversial problems. Thus by means of much study, discussion, and negotiation since the Fur Seal Convention of 1911, a considerable assortment of procedures for handling a variety of international fishery conservation problems have been developed, tested and applied. The United States now is party to eight agreements involving twenty-one nations. The Great Lakes Convention, covering the principal waters of our northern boundary, is the latest addition to this group.

These conventions range from bilateral agreements providing for research in and regulation of a single species, to flexible multilateral agreements covering many species in a given ocean area. Among the features included in one or another of these conventions are provisions for the handling of any joint conservation problem by the signatory nations concerned with that problem; for research and management with special treatment for stocks of fish under full utilization; and for the solution of special problems in cases where the established international commission cannot reach agreement.

Following is a brief commentary concerning each of these agreements:

INTERNATIONAL FUR SEAL AGREEMENTS

The supply of fur seal furs for the world market now comes almost entirely from three small island groups of the north Pacific, where this resource has been maintained as a result of effective international action. The International Fur Seal Convention negotiated in 1911 was the first successful international action to restore and maintain the productivity of a major high-seas aquatic resource. These island groups are the Pribilofs of the Bering Sea, which furnish the major portion of the current supply, the Commander Islands off Kamchatka, and Robben Island off the southern part of Sakhalin Island.

In the latter half of the 19th century, it became clear that extensive killing of seals at sea—pelagic sealing—was depleting the north Pacific seal herds and threatening their survival. Numerous efforts were made to bring the nations bordering the north Pacific together in a joint effort to prevent the destruction of the herds and ensure the preservation of the valuable industry founded upon them, It was not until 1911, however, that the United States, Japan, Russia, and Great Britain (on behalf of Canada) entered into an agreement for the protection of the seals.

Outstanding features of this agreement were the prohibition of pelagic sealing, provision for regulated killing on the rookeries, and provision for the sharing of the proceeds from annual killings among the nations party to the agreement. The agreement did not provide for joint research. Within a relatively short time the beneficial effects of the limitation on killing began to manifest themselves. The downward trend in the seal population reversed itself and by 1916 the population had approximately doubled. By the 1930's, the Pribilof herd had increased to approximately 1½ million individuals.

This convention operated successfully until October 1940, when the Japanese Government notified the other signatories to the convention of its intention to terminate the convention one year thereafter. In its opinion the fur seals of the north Pacific had grown so numerous that the objective of the convention, the protection of fur seals, had been achieved and, on the other hand, the direct and indirect damage inflicted by the fur seals on the fishing industry of Japan was proving more and more serious. Since no new agreement was reached, the convention was terminated on the 23rd of October 1941.

Protection of fur seals was continued through an agreement between the United States and Canada (1942) and the unilateral action of the Government of the U.S.S.R., and later of the Government of Japan after the Japanese Treaty of Peace. The governments of Japan, the U.S.S.R., and Canada have very recently accepted the invitation of the U.S. Government to a conference in Washington, D.C., late in November 1955, to negotiate a new fur seal convention.

PACIFIC HALIBUT CONVENTION

The Halibut Convention between the United States and Canada, negotiated in 1923 to provide for the conservation of halibut of the northeastern Pacific Ocean, was the first successful attempt involving joint action in research, and international conservation management, of a high-seas fishery. Prior to negotiation of the convention the halibut fishery had expanded rapidly, and following that expansion the yields in individual areas had precipitously declined.

Several characteristics of the fishery contributed to the success of the Halibut Convention. The fishery concerned two countries only, and was confined to one species and largely to a single type of fishing operation. However, success was furthered most of all by a realistic and effective research program which determined, then concentrated upon, the lines of research which revealed the relation between the fishery and the stocks of fish, and indicated the management measures which would be most effective. As first negotiated, this convention provided for an international commission empowered to conduct research but not to regulate. The results of the research were so convincing that the convention was renegotiated in 1930 to include provisions which gave the commission the authority to regulate the fishery. This commission has its own research staff, and makes use of an advisory committee of representatives from the halibut industry. The convention provides for equal sharing of the expenses by the United States and Canada.

The Halibut Convention has been further revised—in 1937 and 1953—in order to keep it up to date and permit the most effective handling of its responsibilities.

Following inauguration in 1931 of the management program, the decline in the halibut stocks was halted, and a major increase in productivity has resulted since. From a poundage of 44 millions in 1931, the catch rose to more than 70 million pounds in 1954. This production exceeds that of the early years when the fishery was drawing heavily upon accumulated stocks. About 75 per cent of the world's present supply of halibut is produced from the stocks managed by the Halibut Commission.

PACIFIC SOCKEYE SALMON CONVENTION

The United States and Canada ratified their third effective fishery convention in 1937 to cover the sockeye salmon of the Fraser River. These salmon had been practically wiped out as a result of landslides on the river, and overfishing. The convention provided for regulation after research covering two cycles of the salmon run, or eight years. The costs of the convention are divided equally between the two governments, and the commission is required to regulate the fishery in such a way that the catch is divided as nearly as possible in equal shares between the fishermen of the two countries. After several years of investigation the commission proceeded with the construction of fishways at Hell's Gate and elsewhere, which the commission's investigations had clearly demonstrated were critical to the rebuilding of the salmon runs and, after the lapse of the required eight years, undertook regulation of the fishery.

The commission's work is now showing practical results in the rapid increase in the runs of sockeye. Through the continued operations of this commission it is confidently expected that the runs, worth many millions of dollars annually, will be restored and maintained at maximum productivity. During the peak years of the fishery the production averaged about 20,000,000 fish annually. From this level it was reduced to less than two million. The work of the Commission restored the run in 1954 to about 10,000,000 fish, and it is expected that, under continued sound research and management, runs can be built up to their original level.

INTERNATIONAL WHALING CONVENTION

It has been recognized for some years that unrestricted whaling would deplete or even destroy the world whale stocks, and seriously affect the economy of countries dependent upon this resource for fats and oils. Multilateral agreements for the regulation of whaling have been in effect for more than twenty years, the first having entered into force in 1934. Revised agreements were negotiated in 1937, 1938, 1944, and 1946. The 1946 convention is now in effect with seventeen nations as signatories, including all the major whaling countries.

To the 1946 Convention was annexed a schedule of whaling regulations which is amended from time to time as the whaling commission established by the convention finds necessary. This device, coupled with mandatory reporting of whales killed, and related data, provides the flexibility needed to meet changing conditions in the whale stocks through modification of the open season, closed areas, minimum lengths, and so forth.

The International Whaling Commission, on which all parties to the 1946 convention are entitled to be represented, is the supervising authority under that convention, meeting annually. Its main responsibility relates to amendment of the schedule of whaling regulations. These include fixing of species and minimum lengths of whales which may be taken, open and closed seasons and waters, types of gear permitted, methods of measurement, catch returns, and other statistical and biological records and reports. Additionally, it conducts scientific research on whales and whaling, and reviews enforcement by the contracting parties, on their own nationals, of the obligations deriving from the convention.

Under the provisions of the agreements in force during the period from 1944 to 1953, the annual catch of whales in the Antarctic was limited to 16,000 blue whale units, which represented a reduction by one-third of the catch during six pre-war years. (The blue whale unit is a measure to equivalate the varying sizes of different whale species, e.g. one blue whale unit equals one blue whale or six sei whales, etc.) This was further reduced to 15,000 blue whale units in 1954. During this period the open season for Antarctic whaling has been progressively shortened, and the opening date advanced. All this has been accomplished while the production of whale oil has remained about the same as in 1938–39. The number of whales taken has been reduced to encourage recovery of the stocks from their dangerous low, while oil production has been maintained by increasingly concentrating the season in months when the whales are the fattest, that is, yield the greatest amount of oil per animal.

INTER-AMERICAN TROPICAL TUNA CONVENTION

The results of the halibut and salmon conventions, have encouraged a similar approach to other international high-seas fishery problems. In 1949 the United States negotiated with Costa Rica the Inter-American Tropical Tuna Convention. This convention provides for research on the yellowfin tuna, skipjack, and bait fish found in the waters off the Pacific Coast of the Americas, and for recommending to the contracting parties the conservation measures found necessary. It adds two new features to U.S. fishery treaty practice: (1) The convention is open-ended; that is, any of the nations concerned with these fisheries can adhere to the convention at a later date with the consent of the countries then party to the convention; (2) It provides that the costs of operation shall be divided among the contracting parties in relation to the catch from the fish stocks covered by the convention. It is hoped through this convention eventually to develop the co-operation of all of the eastern Pacific coastal states, off which tuna are found, in a programme of research and, if necessary, regulation. Recently, Panama has adhered to this convention, and is now an active member.

NORTHWEST ATLANTIC FISHERY CONVENTION

For the past two decades many people interested in New England's high-seas fisheries have strongly advocated a fisheries convention among the nations fishing the northwest Atlantic. This finally led to the negotiation in February 1949 of the Northwest Atlantic Fisheries Convention, which convention includes all ten countries from the two sides of the Atlantic whose vessels fish in the area.

Several new features were developed in this convention to handle the special problems arising from so many countries fishing to varying extents in the different parts of the northwest Atlantic area. The convention divides the northwest Atlantic into five sub-areas and provides a separate panel for each sub-area, each panel including representatives only from those nations fishing in the sub-area concerned. It is possible by this means to bring the many separate problems involving the different groups of countries in each sub-area under one over-all convention. This avoids the necessity of a multiplicity of separate agreements. The convention also provides that, when conservation measures recommended by the commission are accepted by all the parties which are members of the panel for a given sub-area, the measures then apply to all parties to the convention. The operations of the commission are financed on the basis of $500 annually from each contracting party, with the remaining costs divided among the parties in proportion to the number of panels on which they are members. In the field of research, the convention provides that the commission, when feasible, shall arrange for the co-operative study of the fishery problems of the area by the countries party to the convention, through preparation and co-ordination of an over-all research program, rather than by operating its own research staff as do the halibut, salmon, and tuna commissions.

NORTH PACIFIC FISHERIES CONVENTION

The north Pacific area includes the three oldest examples of successful international co-operation in the maintenance of the productivity of major aquatic resources—fur seals, halibut, and salmon. It is also an area which has witnessed some of the most severe conflicts and disagreements between the fishermen of different countries in connection with their fishing operations. The fisheries for halibut and salmon of the northeastern Pacific were developed at an early stage because of the strong market demand which resulted in a premium price. The Governments of the United States and Canada have participated in extensive unilateral and joint efforts to study and regulate these fisheries, and to restore and maintain their maximum productivity. It is generally recognized that the continued productivity of these resources is the result of the expenditure of research and funds by the managing governments and the restraints placed upon their own fishermen by an extensive regulatory system. It is generally felt that if these resources, which have been maintained by the contiguous states, could be drawn upon by the fishermen of other countries which had not participated in the research and regulatory programmes, the returns to the regulating countries would be so reduced that they would not be justified in maintaining these expensive programs.

A solution for the problems of this area finally was developed in the North Pacific Fisheries Convention negotiated between Japan, Canada, and United States, and ratified in 1953. This convention was designed to cover all the joint fishery problems of the three contracting parties in the north Pacific area. It concerns all stocks of fish under substantial exploitation by two or more of the contracting parties, with the decisions and recommendations concerning regulation of such stocks being confined to the parties engaged in their substantial exploitation. It sets up a new principle, " abstention ", which provides that, where a stock of fish is being fully utilized by one or more of the contracting parties, and where such parties have enacted and are enforcing fishery conservation regulations and limitations developed through extensive scientific research, other contracting parties not sharing in exploitation of that stock should continue to abstain from participation.

To facilitate the administration of this abstention principle a provisional line was drawn in the north Pacific Ocean to separate the stocks of salmon of American and Asian origin, and a mandate placed upon the commission to undertake immediate research to verify or improve this provisional line. It was further provided that, in the event of the commission failing within a reasonable period of time to reach unanimous agreement on such a line, the matter should be referred to a special committee of scientists consisting of three competent and disinterested persons, no one of whom should be a national of a contracting party, selected by mutual agreement of all parties. Majority determination by such a committee would determine the recommendation to be made by the commission.

OBJECTIVES OF THE CONVENTIONS

The primary objective of the various international fishery conventions, involving north American countries, has been consistently confined to conservation; that is, to making possible the maximum sustainable productivity of the aquatic resources covered by the conventions. It is obvious that such conservation programmes have many economic implications and involve economic considerations. The results of any such program must be in products useful to man, and regulations must be adapted to the practical operations of the fishery. However, the economic considerations have been secondary. The conventions provide for conservation management, not economic management.

POLICIES

In the process of studying the various problems, developing practical solutions, and operating the commissions, certain policies have been evolved and have proved themselves. The principal such policies are the following:

1. *Specific Conventions for Specific Problems*

The fishery conventions have been individually tailored for specific situations and problems. As has been pointed out above, the first conventions covered single species and areas. As the procedures developed for these conventions proved successful, it has been possible to negotiate conventions covering a greater complexity of species and problems and wider areas. The Northwest Atlantic Convention covering all joint fishery conservation problems of the ten countries fishing the northwest Atlantic area, and the North Pacific Convention covering joint problems of the United States, Canada, and Japan in the north Pacific area, are examples of these recent developments.

2. *Selection of Commissioners*
   Members of the various commissions should be selected with respect to the specific commission to which they are appointed. The requirements may vary with the particular commission and stage of its development, so that emphasis is in some cases upon special knowledge of the particular problem, and in others upon general qualifications. It is extremely important that the commissioners have the confidence and support of the public in their respective areas, for such confidence and support is an essential requirement for the success of the commissions. For this reason, in the United States, for example, except for Government members, the Commissioners are appointed from the area affected by the convention.

3. *Advisory Committees*
   Experience in the U.S. with the several commissions has demonstrated the desirability of providing for advisory committees from the public, and interested state governments. They serve a 2-way function. They provide detailed and practical advice to the commission, particularly with respect to the relation between the problems and proposals considered by the commission and the practical operations of the fishery and the state governments. They also serve an invaluable function in informing the various segments of the interested public of the work of the commission and the justification for the various acts which it may perform. In the present commissions they are proving extremely helpful in maintaining public support.

4. *Periodic review of Commission Work*
   Experience has indicated the desirability of providing for a periodic review of the work of a commission by the member parties. This would include a study of progress made in achieving the objectives of the convention, whether the convention served its purpose and should be terminated, or should be continued as before or with modifications which would enable it to more effectively pursue its objectives. A provision of this kind was included in the North Pacific Convention. It is included in a more developed form in the Great Lakes Fisheries Convention. It seems desirable that it should be included in future conventions.

5. *Provision for research under the conventions*
   Two general arrangements for research work are provided under the several conventions. These are to provide: (1) that the commission shall co-ordinate the research work of the contracting parties; or (2) that the commission shall set up its own independent research staff. Co-ordination of the research work of the contracting parties is favoured in situations where the contracting parties involved in the particular problems covered by the convention have established research staffs engaged on these or related problems in the convention area,

unless other considerations govern; for example, if the fishery is located in substantial part off the coasts or in the territorial waters of one party. In the latter case, and in cases where the parties do not have adequate scientific staffs, the use of an independent commission staff has been favoured.

CONCLUSION

It is not possible at present to draft an acceptable over-all convention to cover all areas of the Atlantic and Pacific. It is quite possible that further experience will confirm present indications that such over-all conventions never will be the most effective procedures for handling such problems. Furthermore, it is not likely that the expense of operation of such an over-all convention would be less than the costs of specialized conventions such as exist at present. In fact it might be increased. The maintenance of separate commissions does not involve an increase in the expense of operation through additional travel and working time since, whether one or a group of commissions handled the various problems, the number of regional meetings and travel would not be substantially affected. With an over-all convention it would be much more difficult to focus proper attention on specific problems and to maintain necessary public interest and support.

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Hearing and acoustic orientation in marine animals*

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Summary—The evidence that underwater sound is important in the behaviour of fishes and cetaceans is reviewed, with emphasis on the possible occurrence of acoustic orientation. Both these groups of marine animals have now been shown to have excellent hearing. At least one fish has a minimum auditory threshold of the same order of magnitude as the typical human threshold at 2000–4000 c.p.s. (about 10^{-16} watt/cm^2 energy flux). Porpoises can hear sounds of moderate intensity at frequencies well above 100 kc. A series of recordings which may have resulted from a deep sea fish engaged in echo-sounding are analyzed and discussed, and the possible role of echolocation in marine animals is compared with the available evidence of its nature and occurrence in bats and other animals relying on airbourne sound. In this connection the possible usefulness of continuous sounds and standing wave patterns is discussed with reference to the observed fact that a low frequency sound in a small tank undergoes marked fluctuations in intensity over distances that are a small fraction of its wave-length in water.

In recent years it has become widely recognized that a variety of sounds are produced by animals living in the ocean. The chief cause of this increased awareness has been the use of improved devices for listening to sounds in water. It had been known since the time of Aristotle that some fish produce sounds (for recent pre-war studies see Tower, 1908; Burkenroad, 1931; Dijkgraaf, 1932; and Hardenberg, 1934). But the unaided human ear is at a great disadvantage in listening to underwater sounds, and hence only those of considerable intensity can be heard without devices to provide us with a sensitivity to sound waves in water that approaches our sensitivity for sounds arriving through the air. Such devices have been developed primarily for military purposes, and it was during the second World War that sounds of fish and other marine animals first aroused serious concern when they interfered with underwater listening operations. Surveys were therefore undertaken to determine the sources and seasonal occurrence of the more intense of these biological noises (Loye and Proudfoot, 1946; Dobrin, 1947; Knudsen, Alford, and Emling, 1948). Since the war such surveys have continued on a broader basis with greater attention to their biological significance (Johnson, Everest, and Young, 1947; Johnson, 1948; Fish, Kelsey, and Mobray, 1952).

As a result of these studies it is now clear that sounds of considerably greater intensity than the ambient background noise level of the ocean are commonly produced by three major groups of animals: (1) many species of fish, (2) several species of marine mammals—certainly some of the smaller whales and porpoises and perhaps some of the larger whales as well, and (3) the snapping shrimps of the genera *Crangon* and *Synalpheus* among the Crustacea. Too little is known about the significance of the " snap " of these shrimps to warrant any discussion of it, and indeed the one serious study to date has led to the conclusion that the noise may well be incidental to some other function of these animals' highly modified claws (Johnson, Everest, and YOUNG, 1947). But the sounds of fish and marine mammals are so numerous, so intense, and so diversified, that a review of what is known concerning their biological significance is timely. While only a small minority of the known species of fish emit sounds that are more than mere by-products of other activities (such as the grinding of teeth), many of those that are consistent noisemakers have specialized structures for the generation of sound, such as muscles located in the walls of the swim bladder. It therefore seems likely that these sounds serve some definite purpose in the lives of the fish that make them. Cases are known in which fish are attracted by sound (WESTENBERG, 1953), but more often they are repelled by artificially generated sounds, while under many circumstances they show no discernible reactions at all. Some species apparently communicate with each other by means of sound, for example the toadfish *Opsanus tau*, in which the male calls principally during the breeding season. There is suggestive evidence to be discussed below that orientation may be maintained with respect to the bottom by a process akin to echo-sounding; and it is not beyond the bounds of possibility that fish or marine mammals may employ a sort of natural sonar—an underwater analog of the process of echolocation so highly developed by bats for use in air. Questions of this type deserve more attention than they have yet received, and the chief purpose of this paper is to review the available evidence of acoustic orientation by marine animals and to suggest promising lines of inquiry for the future. It is particularly appropriate that such a review should be part of a volume dedicated to Professor BIGELOW, for he contributed significantly, in 1904, to the basic biological knowledge that has formed an essential groundwork for these recent developments.

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The sensitivity of hearing in fish

Fundamental to any consideration of the role of underwater sound in orientation, or in other types of behaviour, is the question of sensory capacities of the animals concerned. No animal can react to a sound it cannot hear, and even the author of an authoritative textbook recently wrote, in introducing the auditory system, " Through the long and complex evolution of the fishes no progress was made, since no auditory receptors exist. . . . Fish do not hear, and there would be little to hear under water . . . Hearing is developed on the assumption of terrestrial life, hence, is first encountered in the amphibia " (KRIEG, 1942). Even when a particular species has been shown, qualitatively, to be able to react to underwater sound, any careful analysis of its behaviour is likely to require quantitative measurement of the range of frequencies and intensities that it can hear. It was to this basic question that BIGELOW addressed himself more than fifty years ago.

There was already observational and anecdotal evidence that certain fish reacted to sound, usually to sounds generated in air. On the other hand several attempts to demonstrate hearing in fish under controlled conditions had produced negative results, or at best ambiguous evidence. Among the more recent of these investigations had been those of KREIDL (1895, 1896), who had a few years previously carried out in SIGMUND EXNER's laboratory in Vienna one of the classic experiments of comparative physiology (the substitution of iron filings for sand grains in the equilibrium organs of certain shrimps, so that the action of the statoliths could be demonstrated unequivocally by the use of a magnet). KREIDL had observed the responses of goldfish (*Carassius auritus*) to sounds of moderately low frequency, but the fish responded just as well after the inner ear had been exposed and the semi-circular canals plucked out with forceps—a procedure which seemed likely to damage the organs of hearing. Hence Kreidl concluded that goldfish detect underwater sound not by means of the inner ear but through mechanical receptors of the lateral line or skin.

Bigelow repeated Kreidl's experiments, working under the guidance of the late G. H. Parker, who had just demonstrated the auditory sensitivity of *Fundulus*, and he extended them with a simple elegance of experimental design which merits the respectful consideration of current investigators. Having found that his goldfish responded more than 80% of the time when stimulated by a 100 c.p.s. tuning fork, he cut virtually the entire sensory nerve supply to the skin and lateral line, and still observed almost the same percentage of responses. Yet when both eighth cranial nerves were cut there were no responses in 73 trials with seven different goldfish. As a control against side effects of exposing and cutting the auditory nerve, both eighth nerves were exposed but only one was cut; this fish still responded to sound, but ceased to do so when the remaining auditory nerve was severed. In another control the spinal cord, lateral line nerves, and the cutaneous branches of cranial nerves V and VII were cut without effect on the response to sound. Bigelow went on to repeat Kreidl's operation, and he obtained the same result. But he also found from histological sections that plucking out the semi-circular canals left much of the sacculus and lagena intact, these being the portions of the ear that would be expected to play the major role in responses to sound. Q.E.D.: goldfish could hear.

Like many biological problems the question of hearing in fish underwent a long subsequent history of complications and controversies, and a generation later an active debate still centred around the simple question, " can fish hear, and if so, what ? " (For complete reviews see von Frisch, 1936, and Kleerekoper and Chagnon, 1954). In many of the earlier experiments spontaneous responses were obtained from fish when vibrations of various frequencies and intensities were imparted to the water by a wide variety of methods. In other cases fish were conditioned or trained to give responses when the water around them was set into oscillation, and considerable evidence pointed to the importance of the lateral line and the skin, especially for low frequencies (Parker and van Heusen, 1917). The methods used to generate underwater sound in these earlier experiments were (1) to generate the sound in air near the tank containing the fish, (2) to place a vibrating object such as a tuning fork in contact with the tank, or (3) to immerse a buzzer or telephone receiver in the water itself. In all cases the stimulus undoubtedly set the water into vibrations with a complex frequency spectrum, but the component most obvious to the experimenter may not have been the one which was most effective in stimulating the fish. This situation was greatly clarified by the careful work of von Frisch and his associates from 1929 to 1941; and although most of the experiments employed freshwater fish, important general conclusions were reached which can be applied directly to marine species, as has recently been demonstrated by Dijkgraaf (1952).

Stetter reported in 1929 that two common freshwater fish, (the European minnow, *Phoxinus laevis*, and the common catfish, *Ameiurus nebulosus*) could be trained to come for food to a particular part of the tank (or to give other characteristic feeding movements) when a sound was produced in the air at some distance from the aquarium. The fish were blinded to prevent them from responding to visual rather than auditory stimuli associated with feeding. Clear responses were obtained from sounds generated by tuning forks, whistles, and pipes, even when the frequency was as high as 6,960 c.p.s. with the minnows, and 13,139 c.p.s. with the catfish.

VON FRISCH and STETTER (1932) later experimented with the effects of sensory impairments on the ability of minnows to respond to various frequencies. Damage to the utriculus and semicircular canals caused little reduction in sensitivity to sounds, although equilibrium was severely impaired. But when the sacculus and lagena were put out of action the sensitivity to frequencies above 150 c.p.s. was almost totally destroyed. Even frequencies as low as 32 c.p.s. were less effective in arousing responses than when the sacculus and lagena were intact. Very low frequencies such as 16 c.p.s., however, were almost as easily perceived as they had been before the operation. Nor did impairment of the lateral line receptors reduce the fishes' sensitivity to low frequencies. These investigators therefore concluded that low frequencies must be detected through very sensitive tactile receptors in the skin (see also REINHARDT, 1935).

Absolute thresholds could not be determined in these experiments, because no calibrated underwater transducers were available for the purpose. In an attempt to obtain approximate thresholds, the source of the stimulating sound was moved to greater and greater distances from the aquarium, and the threshold of response of the fish was compared with the threshold of hearing of men standing beside the aquarium. The fish ceased to respond at levels somewhat above the human threshold; but when a man was held entirely underwater in a large aquarium, he was unable to hear the sound at intensities to which the minnows would still react.

In later experiments at the same laboratory by BOUTTEVILLE (1935) and DIESSELHORST (1938) the sound was generated by a loudspeaker close to the aquarium, and its intensity *in the air* was measured by means of a calibrated microphone. The threshold of response of a fish could thus be expressed in terms of sound pressure in the air just outside of the glass-walled aquarium. The most sensitive of the minnows gave consistent responses to 652 c.p.s. when the sound level in the air was 20 decibels above the customary reference level of 0·0002 dynes/cm^2, or ten times the threshold sound pressure for a typical human listener. This is a remarkable sensitivity when one considers that the energy loss was unquestionably great as the sound waves passed from air to water. I once duplicated approximately the acoustic conditions of this type of experiment and measured sound pressures inside the aquarium with a calibrated hydrophone while those in the air were measured with a calibrated condenser microphone. The sound pressures in air and water were roughly the same (within 5 to 10 decibels). But the greater acoustic impedance of water causes a given sound pressure to correspond in water to a 35 db lower energy flux (watts·cm^2) than in air. This means that the minnows studied by VON FRISCH and his associates had auditory thresholds of the same order of magnitude, in terms of energy flux, as the human auditory threshold in air.

When a number of species were compared with the minnow *Phoxinus* with respect to their sensitivity and frequency range of hearing, it became clear that fish can be divided into two distinct groups. The minnow *Phoxinus*, the catfish *Ameiurus*, and certain other fish, display low thresholds and a wide frequency range, while the other fishes studied were less sensitive and responded only to frequences below 1000–2000 c.p.s. This difference is correlated with the anatomy of the fish; for the more sensitive species have an air-filled chamber directly coupled to the inner ear labyrinth. In the order *Ostariophysi* (families *Cyprinidae*, *Characinidae*, *Siluridae* and *Gymnotidae*) this involves the Weberian apparatus, an intricate structure consisting of bones, cartilages and air ducts which serve to effect a mechanical coupling between the swim bladder and the inner ear. VON FRISCH and STETTER (1932) demonstrated experimentally that the minnow suffered a considerable hearing loss when this mechanism was damaged surgically. Air chambers can improve the sensitivity of fish's hearing because sound travels almost without disturbance from one aqueous medium to another, and the soft tissues of any animal are so much like water in their acoustical properties that a " pure " fish is relatively " transparent " to underwater sound. An air bubble or an air-filled chamber, on the other hand, represents a marked acoustical discontinuity much as does a solid object in the air. For a detailed consideration of the acoustical properties of the catfish swim bladder see POGGENDORF (1952). Other fishes with keen hearing also have some type of air chamber coupled to the inner ear. These structures have different morphological origins, but seem to serve the same auditory function as the swim-bladder and its ramifications in the *Ostariophysi*.

This anatomical correlation is an important one; for it permits one to predict with some confidence that fish possessing structures that connect some air-filled chamber with the inner ear labyrinth will have keen hearing. Among marine fish there are very few groups which have such accessory organs of hearing. The sea catfishes are anatomically similar to the freshwater catfish *Ameiurus*, and they might be expected to have keen hearing on that account. In this connection it is interesting to note that sea catfishes are listed among the species reported by BURKENROAD (1931) and DOBRIN (1947) as significant producers of underwater noise. The herrings (family Clupeidae) are another group which one would expect to have keen hearing because of their auditory structures, which have been described by RIDGEWOOD (1891), WOHLFAHRT (1936), and EVANS (1940). There is an elaborate set of air passages extending from the air bladder into close apposition with the membraneous labyrinth of the inner ear. There are also reports that herrings are easily frightened by noises made in fishing boats. Since the herring family is an abundant marine group having great commercial importance, their ability to hear various frequencies of underwater sound merits quantitative investigation.

Two recent investigations have included quantitative measurements of auditory thresholds in fish, and the results have amply confirmed the earlier conclusions of VON FRISCH and others regarding the approximate equality of auditory thresholds in fish and men, when expressed in terms of energy flux (watts/cm^2). AUTRUM and POGGENDORF (1951) and POGGENDORF (1952) used a calibrated Rochelle salt crystal to measure the sound pressure in a small aquarium containing single catfish (*Ameuirus nebulosus*), and they determined auditory thresholds at frequencies from 60 to 10,000 c.p.s. The threshold values varied considerably, but the average of the measurements at a given frequency is probably valid within ± 10 db. KLEEREKOPER and CHAGNON (1954) have estimated auditory thresholds of a small cyprinid fish, the creek chub *Semotilus atromaculatus*, and they report a rather narrow range of maximum sensitivity, the thresholds being lowest at about 300 c.p.s. and rising by tenfold at 100 and at 2000 c.p.s. In view of the absolute, though approximate, calibration of the measuring instruments used by AUTRUM and POGGENDORF, their data for the catfish provide the best available evidence concerning the sensitivity of hearing in fish to underwater sound. They found the auditory threshold to be approximately constant from 60 to 1600 c.p.s. at slightly above 0·01 dyne/cm^2 or approximately 10^{-16} watt/cm^2. This threshold energy flux corresponds closely to the minimum human threshold in air (between 2000 and 4000 c.p.s.), but the catfish is considerably more sensitive at lower frequencies. Above about 2000 c.p.s., on the other hand, this fish's threshold rises much more steeply than the human threshold.

AUTRUM and POGGENDORF also demonstrated that the catfish's responses depended upon sound pressure rather than amplitude or particle velocity. They confirmed the earlier qualitative findings of VON FRISCH *et al.* that fish without air bladders have thresholds roughly 30 db higher than the catfish. Other experimenters have reported that the Ostariophysii at least can discriminate between sounds differing in frequency by as little as 1/4 octave (WOHLFAHRT, 1939; DIJKGRAAT and VEREIJEB, 1949; and KLEEREKOPER and CHAGNON, 1954). Directional sensitivity, or the ability to localize the source of an underwater sound, has not yet been adequately demonstrated, and indeed both REINHARDT (1935) and VON FRISCH and DIJKGRAAF (1935) obtained negative results in attempts to demonstrate localization of sound sources by stationary fish. On the other hand, KLEEREKOPER and CHAGNON concluded, on the basis of extensive observations and photography of the movements of *Semotilus* in a tank approximately one metre square, that these small members of the order *Ostariophysii* could immediately turn towards the louder of two equidistant sources of 50 c.p.s. sound.

A possible case of echo-sounding in fish

Having thus reviewed the overwhelming evidence for a high degree of auditory sensitivity in fish, it must be admitted that very little critical evidence is available to indicate what significance sound may have in fish behaviour. Rather than summarizing unsatisfactory anecdotal evidence I shall merely describe one observation that suggests the occurrence of echo-sounding by a deep sea fish, with the hope that the need for substantial and imaginative investigation of auditory behaviour in fish will thus be emphasized. I am indebted to Dr. J. B. HERSEY of the Woods Hole Oceanographic Institution for permission to make a detailed study of a series of underwater sound recordings made north of Puerto Rico in water approximately 5100 metres deep. Among many hours of recordings made far from land, that include noises of biological origin, those made about 3 p.m. on March 7, 1949 contain several loud calls, each followed after a short interval by a fainter repetition of itself. In listening to these sounds, it is difficult to avoid the impression that they are the calls of some marine animal followed by echoes of these calls. While no similar calls and apparent echoes have been noted subsequently, as far as I can ascertain, a brief analysis of this recording is of interest.

The instruments used were a crystal hydrophone, amplifiers, filters, and recording equipment sensitive to 50–1200 c.p.s. The hydrophone was within 70 feet of the surface, and the background noise level was 75–80 db above 0·0002 dyne cm^2. The calls of what was dubbed the " echo fish " consisted of short notes lasting 1/3 to 1·5 seconds, and having a rather constant frequency of about 500 c.p.s. The apparatus was not precisely calibrated, but the calls were typically two to three times the background noise level, and occasionally the signal-to-noise ratio was as high as seven. The interval between the loud call and its faint repetition was quite constant, and when the recording was played through a 500 c.p.s. tuned filter both the call and the apparent echo could be seen clearly in oscillographic records. When the intervals between peaks of original call and apparent echo were measured in 11 oscillographic records showing the highest signal-to-noise ratio, the average interval was 1·58 seconds, the extremes being 1·47 and 1·77 seconds ($\sigma = 0{\cdot}08$ second). The ratio of amplitudes of the apparent echo and original call averaged 0·405, the extreme values of this ratio being 0·27 and 0·56.

If these recordings do indeed consist of calls and echoes, the time interval between them, together with the amplitude ratio and the known depth of 5100 metres, establishes certain geometrical requirements for the location of the " echo fish ". The difference in length of the direct path from source to hydrophone and the path followed by sound waves reflected from the bottom was approximately 2400 metres (the distance travelled by underwater sound in 1·58 seconds). In the simplest case we might assume that the source was directly below the hydrophone, so that its distance above the bottom would be 1200 metres or 3900 metres below the surface. If we make the further assumption that in these cases, when the bottom reflection was maximal, the angles of incidence and reflection were equal, the possible locations of the source are limited to a locus having the form of a shallow dish-like surface with its deepest point 3900 metres below the hydrophone and gradually rising towards the surface as the source is assumed to be displaced laterally. Unless one assumes the source to have been some miles away it must have been at a considerable depth, probably well below the levels to which light can penetrate, and below the depths reached by whales or other marine mammals. These geometrical relationships are thus consistent with the hypothesis that this recording reveals a deep sea fish emitting calls loud enough for them and their echoes from the bottom to be audible at the surface three to four thousand metres away.

This explanation of the " echo fish " recordings can be considered only as a speculative possibility, however, until means are devised to explore the depths of the ocean in greater detail, both acoustically and biologically. Alternate explanations for the sounds recorded in this instance are: (1) that a single fish emitted a double call, (2) that the second call came from a different fish, or (3) that the sounds had a non-biological origin. The third alternative seems quite unlikely because this type of sound was heard on several occasions during the day the recording was made, because it became louder and fainter from minute to minute, and because it was recorded when the ship was many miles from land or other ships under conditions when all possible precautions had been taken to avoid sound production by the ship herself. Reflections from other surfaces than the bottom are rendered most unlikely by the relatively high amplitude ratio and the difference of 2400 metres in path length for the direct and reflected sound. Finally it must be pointed out that even though this recording does reveal a fish call plus its echo from the bottom, we have no direct evidence that the unknown fish could hear such an echo, and still less that it would pay any attention if it did. Yet the " echo fish " could easily have heard these bottom echoes if it had an auditory sensitivity equal to that of any fish adequately studied to date, and in the unlighted depths of the ocean echolocation could be as advantageous to a fish as it is to a bat flying in darkness through the air. We are dealing here with one of many phenomena pertaining to the deeper layers of the ocean concerning which we can only speculate, and dream of future investigations by methods yet to be devised.

Sounds and hearing of marine mammals

A variety of complex sounds are produced by several species of the smaller toothed whales, porpoises, and dolphins. As in the case of fish, a few observations of noises from cetaceans had been reported many years ago, but only during and after the war was it realised how vociferous some of them actually were. The white whale or beluga *Delphinapterus leucas* had long been known to make noises, for these could be heard in the air or through the hull of a ship; and SCHEVILL and LAWRENCE (1949) have described and analyzed in some detail their large vocabulary that includes whistles, squeals, chirps, clicks, and rasping noises. Several other species of porpoises and dolphins have also been studied in captivity or under natural conditions, and all appear capable of producing sounds (SCHEVILL and LAWRENCE, 1949; KRITZLER, 1952). The baleen whales, on the other hand, have not yet been definitely shown to emit sound, although there have been reports from several observers of loud, low pitched notes heard when humpback whales (*Megaptera nodosa*) were in the vicinity.

Excellent hearing has been demonstrated in porpoises and other cetaceans ranging in size up to the pilot whale or " blackfish " *Globicephala macrorhyncha* (KELLOGG and KOHLER, 1952; SCHEVILL and LAWRENCE, 1953; KRITZLER, 1954). While auditory thresholds have not yet been measured, the observational evidence is adequate at least for the bottlenosed porpoise *Tursiops truncatus* to demonstrate that sensitivity of hearing is high. In the most carefully controlled of these studies, SCHEVILL and LAWRENCE trained a *Tursiops* to come for food when it heard pure tones of short duration generated without switching transients or clicks. The intensity level was of the order of 10^{-12} watt/cm^2 or 1 dyne/cm^2, and this porpoise learned to respond almost every time the tone was sounded in the frequency range from 150 c.p.s. to 120 kc, i.e. the animal's auditory threshold was below this level over a very wide range of frequencies. Above 120 kc. the percentage of positive responses fell rather rapidly to less than 20% at 150 kc.

Since marine mammals are often active at night or in turbid waters, it is natural to suggest, as KELLOGG, KOHLER, and MORRIS (1953) have done, that some of their complex and impulsive sounds may be used for echolocation, either to maintain orientation with respect to the bottom, surface, or large obstacles, or possibly to locate fish or other prey in the water as bats appear to do in the air (GRIFFIN, 1953 A). KELLOGG *et al.* have shown that certain of the noises emitted by these porpoises have components of considerable amplitude as high in frequency as 120 kc, and some energy as high as 170 kc; and when intense sounds of short duration are generated in the water there will of course be echoes from any solid objects in the vicinity. Since porpoises have a high degree of adaptability and intelligence as well as keen hearing (MCBRIDE and HEBB, 1948; WOOD, 1953; and LAWRENCE and SCHEVILL, 1954) it is plausible to infer that they might take advantage of the possibilities of echo ranging. No direct evidence has yet been forthcoming, however, to support this inference; and indeed SCHEVILL and LAWRENCE report that porpoises remained silent, as far as could be discerned, even during long periods of swimming about through turbid water where it would seem that echolocation would have been most helpful. It may well be that porpoise sounds are used solely or primarily for communication, especially since solitary porpoises seem ordinarily to be silent. Yet the observation of MCBRIDE (in press) that porpoises can avoid small mesh but not large mesh nets in turbid waters points towards some type of acoustic orientation.

It is pertinent to recall in this connection that the critical evidence that bats (and at least one species of bird) employ echolocation is not alone their production of sound but, more important, their ability to fly without seeing and the disorientation caused by impairment of hearing or sound production (GRIFFIN and GALAMBOS, 1941; GRIFFIN, 1953 B). Comparable experiments are obviously more difficult with cetaceans, but observations of blinded porpoises, or even the use of intense interfering noises, should permit a resolution of this question. It is even possible that porpoises use fainter sounds for echolocation than those studied to date, and that more sensitive apparatus, or improved signal-to-noise ratios, would disclose a more continuous emission under conditions where vision is restricted. The most intense high-frequency sounds of bats are not the pulses used for echolocation, but the noisy cries of much longer duration (which are audible owing to minor low frequency components even though most of their energy is at frequencies above 20 kc). Prolonged listening to bats with relatively insensitive equipment in the presence of moderately high noise levels at ultrasonic frequencies might well have led to a picture of their sounds not unlike our present information that porpoise sounds are numerous, loud, and varied, but often not detectible when needed for acoustic orientation. This comparison is especially relevant for those species of neotropical bats that feed on fruit and orient themselves adequately by means of faint pulses which can easily be overlooked even with reasonably adequate apparatus (GRIFFIN and NOVICK, 1955). All of these considerations warrant an open mind regarding the role of acoustic orientation in marine mammals, and further careful investigation of the matter is clearly called for.

Discussion

In most considerations of the possibility that marine animals orient themselves by echolocation it has been assumed that they would use an analogue of pulse sonar, emitting sounds of very short duration and hearing echoes arriving in the silent intervals between the pulses. Pulsed sounds are employed in the echolocation of all the bats studied to date, although in bats of the family *Rhinolophidae* the pulses may last about 100 msec, so that there must be considerable overlap between outgoing sound and returning echo (MÖHRES, 1953). While some of the sounds emitted by fish and cetaceans consist of rapidly repeated clicks, others are continuous tones or noises; and since sound travels faster in water than in air most of the known fish and porpoise sounds seem poorly suited for echolocation owing to the inevitable mixing of echoes with the outgoing sound. In this regard " echo fish " discussed above, and certain ticking sounds of uncertain origin recorded during Woods Hole Oceanographic Institution cruises, seem to be exceptions to the general rule. It is quite possible, however, for echolocation to be based upon continuous sound, but since the echoes will almost always be fainter than the outgoing sound some special means must be employed to discriminate between the two—frequency as in the case of frequency modulated radar, or the high degree of isolation of the ear from the source of the emitted sound that MÖHRES postulates for the bats of the family *Rhinolophidae*, which use 100 msec pulses to detect objects at such close range that echoes begin to return in 5–10 msec.

There is another aspect of underwater sounds which might be related to echolocation, and which has not been thoroughly considered. The wave lengths of the sounds emitted by most fish, and those to which they are most sensitive, range from about one to ten metres. Most of these sounds last for at least one second, so that in the immediate vicinity of the fish there is ample time for interference and reinforcement between successive waves to be set up, especially if it is close to the bottom or to other solid objects, as is very often the case. At first thought one would expect the principal nodes of such standing waves to be separated by distances equal to the wavelength in water of the particular frequency involved; for 500 c.p.s. this would mean nodes roughly three metres apart. Yet when I have arranged apparatus to generate sounds of a few hundred c.p.s. in small tanks, and measured the resulting sound levels with a hydrophone, there have always been wide fluctuations in the sound pressure over distances that were only a very small fraction of the wavelength. (See also POGGENDORF, 1952, and KLEEREKOPER and CHAGNON, 1954, for similar observations.) The physical basis for these variations in sound level is no doubt somewhat complex, perhaps involving interactions between sound waves in the water and in the materials of which the tank is constructed. Comparable conditions would not ordinarily prevail in the open ocean, but they must often occur near the bottom, rocks, or other hard objects.

Since fish have keen hearing, they must experience fluctuations in the loudness of whatever sounds are present as they swim about in the proximity of any major acoustic discontinuity, and indeed their own movements would alter the standing wave patterns. Since such changes in sound level bear some relation to the geometry of the fish's environment, it is possible that they could learn to use them for orientation (for evidence that fish can easily learn to react to sounds see BULL, 1928, and HARALSON and BITTERMAN, 1950). Presumably such standing wave patterns would be simpler, and hence more readily interpreted by fish, if they were caused by relatively pure tones. DIJKGRAAF (1933, 1947) and KRAMER (1933) have described in fish and amphibians respectively a type of orientation based on very low frequency sounds or vibrations (or even perhaps static pressure). The sense organs involved are those in the skin or lateral line, rather than the ear. This type of orientation which DIJKGRAAF calls "*Ferntastsinn*" seems limited to distances of much less than one metre. At higher frequencies the specialized inner ear and accessory structures provide a much greater sensitivity, and hence a potentially greater range of acoustic orientation. It therefore seems desirable to devote some future research to testing the possibility that fish or cetaceans orient themselves by reacting to the complex standing wave patterns set up in water near solid objects.

Whether such a type of acoustic orientation would be based on variations in sound fields generated by the fish itself or those from other sources, if it occurs at all, can only be learned by further investigation. As stimuli for such investigations the attention of interested readers is called to the papers of SUPA, COTZIN, and DALLENBACH (1944), COTZIN and DALLENBACH (1950), and TWERSKY (1951) for convincing evidence that blind men detect obstacles by acoustic orientation based on a variety of continuous sounds, including pure tones. Furthermore LISSMANN has reported that certain fish orient themselves by means of *electrical* fields of their own making, apparently sensing in some manner yet to be explained the changes in electrical field due to the proximity of objects differing from water in dielectric properties. (See LISSMANN, 1951, and GRAY, 1953, for preliminary accounts of these remarkable findings concerning which no complete report has yet been published). In view of the existence of such modes of orientation we should be prepared to find cases of acoustic orientation in fish or marine mammals based either upon pulsed or continuous sounds.

REFERENCES

Autrum, H. and Poggendorf, D. (1951), Messung der absoluten Hörschwelle bei Fischen (*Ameiurus nebulosus*). *Naturwissenschaften*, **18**, 434–435.

Bigelow, H. B. (1904), The sense of hearing in the goldfish, *Carassius auratus*. *Amer. Natur.*, **38**, 275–284.

Boutteville, K. von (1935), Untersuchungen über den Gehörsinn bei Characiniden und Gymnotiden und den Bau ihres Labyrinthes. *Z. Vergl. Physiol.*, **22**, 162–191.

Bull, H. O. (1928), Studies on conditioned responses in fishes. *J. Mar. Biol. Assoc., U.K.*, n.s., **15**, 485–533.

Bull, H. O. (1930), Studies on conditioned responses in fishes. II. *J. Mar. Biol. Assoc., U.K.*, n.s., **16**, 615–637.

Burkenroad, M. D. (1931), Notes on the sound-producing marine fishes of Louisiana. *Copeia*, 1931, 20–28.

Cotzin, M. and Dallenbach, V. M. (1950), " Facial vision ": the role of pitch and loudness in the perception of obstacles by the blind. *J. Psychol.*, **63**, 485–515.

Diesselhorst, G. (1938), Hörversuche an Fischen ohne Weberschen Apparat. *Z. Vergl. Physiol.*, **25**, 748–783.

Dijkgraaf, S. (1932), Über Lautäusserungen der Elritze. *Z. Vergl. Physiol.*, **17**, 802–805.

Dijkgraaf, S. (1933), Untersuchungen über die Funktion der Seitenorgane an Fischen. *Z. Vergl. Physiol.*, **20**, 162–214.

Dijkgraaf, S. (1947), Über die Reizung des Ferntastsinnes bei Fischen und Amphibien. *Experientia* **3**, 206–208.

Dijkgraaf, S. (1952), Über die Schallwahrnehmung bei Meeresfischen. *Z. Vergl. Physiol.*, **34**, 104–122.

Dijkgraaf, S., and Verheijen, F. J. (1949), Neue Versuche über das Tonunterscheidungsvermögen der Elritze. *Z. Vergl. Physiol.*, **32**, 248–256.

Dobrin, M. B. (1947), Measurements of underwater noise produced by marine life. *Science*, **105**, 19–23.

Evans, H. M. (1940), *Brain and body of fish.* Blakiston Co., Philadelphia, 164 pp.

Fish, M. P., Kelsey, A. S., Jr., and Mowbray, W. H. (1952), Studies on the production of underwater sound by North Atlantic coastal fishes. *J. Mar. Res.*, **11**, 180–193.

Frisch, K. von (1936), Ueber den Gehörsinn der Fische. *Biol. Rev.*, **11**, 210–246.

Frisch, K. von and Dijkgraaf, S. (1935), Können Fische die Schallrichtung wahrnehmen? *Z. Vergl. Physiol.*, **22**, 641–655.

Frisch, K. von, and Stetter, H. (1932), Untersuchungen über den Sitz des Gehörsinnes bei der Elritze. *Z. Vergl. Physiol.*, **17**, 686–801.

Gray, James (1953), *How animals move.* Cambridge Univ. Press, p. 37.

Griffin, D. R. (1953 a), Bat sounds under natural conditions with evidence for echolocation of insect prey. *J. Exp. Zool.*, **123**, 435–466.

Griffin, D. R. (1953 b), Acoustic orientation in the oil bird, *Steatornis*. *Proc. Nat. Acad. Sci.*, **39**, 884–893.

Griffin, D. R. and Galambos, R. (1941), The sensory basis of obstacle avoidance by flying bats. *J. Exp. Zool.*, **86**, 481–506.

Griffin, D. R. and Novick, A. (1955), Acoustic orientation in neotropical bats. *J. Exp. Zool.* (in press).

Haralson, J. V. and Bitterman, M. E. (1950), A lever depression apparatus for the study of learning in fish. *Amer. J. Psychol.*, **63**, 250–256.

Hardenberg, J. D. F. (1934), Ein tone erzeugender Fisch. *Zool. Anzeiger*, **108**, 224–227.

Johnson, M. W. (1948), Sound as a tool in marine ecology, from data on biological noises and the deep scattering layer. *J. Mar. Res.*, **7**, 443–458.

Johnson, M. W., Everest, F. A. and Young, R. W. (1947), The role of snapping shrimp (*Crangon* and *Synalpheus*) in the production of underwater noise in the sea. *Biol. Bull.*, **93**, 122–138.

Kellogg, W. N., Kohler, R. and Morris, H. N. (1953), Porpoise sounds as sonar signals. *Science*, **117**, 239–243.

Kellogg, W. N. and Kohler, R. (1952), Responses of the porpoise to ultrasonic frequencies. *Science*, **116**, 250–252.

Kleerekoper, H. and Chagnon, E. C. (1954), Hearing in fish with special reference to *Semotilus atromaculatus atromaculatus* (Mitchell). *J. Fish. Res. Bd., Canada*, **11**, 130–152.

Knudsen, V. O., Alford, R. S. and Emling, J. W. (1948), Underwater ambient noise. *J. Mar. Res.*, **7**, 410–429.

Kramer, G. (1933), Untersuchungen über die Sinnesleistungen und das Orientierungsverhalten von *Xenopus laevis* Daud. *Zool. Jahrb., Abt. Allg. Zool. u. Physiol. d. Tiere*, **52**, 629–679.

Kreidl, A. (1895), Ueber die Perception der Schallwellen bei den Fischen. *Pflügers Arch. f. d. Ges. Physiol.*, **61**, 450–464.

KREIDL, A. (1896), Ein weiterer Versuch über das angebliche Hören eines Glockenzeichens durch die Fische. *Pflügers Arch. f. d. Ges. Physiol.*, **63**, 581–586.
KREIG, W. J. S. (1942), Functional neuroanatomy. *Blakiston Co., Philadelphia*, 553 pp.
KRITZLER, H. (1952), Observations on the pilot whale in captivity. *J. Mammal.*, **33**, 321–334.
LAWRENCE, B. and SCHEVILL, W. E. (1954), *Tursiops* as an experimental subject. *J. Mammal.*, **35**, 225–232.
LISSMANN, H. W. (1951), Continuous electrical signals from the tail of a fish, *Gymnarchus niloticus* Cuv. *Nature*, **167**, 201–202.
LOYE, D. P. and PROUDFOOT, D. A. (1946), Underwater noise due to marine life. *J. Acoust. Soc., Amer.*, **18**, 446–449.
MCBRIDE, A. F. (in press). Evidence for echolocation by cetaceans. *Deep-Sea Res.* **3** (2).
MCBRIDE, A. F. and HEBB, D. O. (1948), Behaviour of the captive bottle-nose dolphin, *Tursiops truncatus*. *J. Comp. Physiol. Psychol.*, **41**, 111–123.
MÖHRES, F. P. (1953), Über die Ultraschallorientierung der Hufeisennasen (Chiroptera – Rhinolophinae). *Z. Vergl. Physiol.*, **34**, 547–588.
PARKER, G. H. (1903), Hearing and allied senses in fishes. *Bull. U.S. Bur. Fish. Comm.*, **22**, 45–64.
PARKER, G. H. and VAN HEUSEN, A. P. (1917), The reception of mechanical stimuli by the skin, lateral line organs and ears in fishes, especially *Ameiurus*. *Amer. J. Physiol.*, **44**, 463–489.
POGGENDORF, D. (1952), Die absoluten Hörschwellen des Zwergwelses (*Ameiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparates der Ostariophysen. *Z. Vergl. Physiol.*, **34**, 222–257.
REINHARDT, F. (1935), Über Richtungswahrnehmung bei Fischen, besonders bei der Elritze (*Phoxinus laevis L.*) und beim Zwergwels (*Amiurus nebulosus* Ruf.) *Z. Vergl. Physiol.*, **22**, 570–603.
RIDGEWOOD, W. G. (1891), The air-bladder and ear of British clupeoid fishes. *J. Anat. and Physiol.*, **26**, 26–42.
SCHEVILL, W. E. and LAWRENCE, B. (1949), Underwater listening to the white porpoise (*Delphinapterus leucas*). *Science*, **109**, 143–144.
SCHEVILL, W. E. and LAWRENCE, B. (1953), Auditory response of a bottlenosed porpoise, *Tursiops truncatus* to frequencies above 100 kc. *J. Exp. Zool.*, **124**, 147–166.
STEFFER, H. (1929), Untersuchungen über den Gehörsinn der Fische, besonders von *Phoxinus leavis* L. and *Amiurus nebulosus* Raf. *Z. Vergl. Physiol.*, **9**, 339–477.
SUPA, M., COTZIN, M. and DALLENBACH, K. M. (1944), " Facial vision ": the perception of obstacles by the blind. *Amer. J. Psychol.*, **57**, 133–183.
TOWER, R. W. (1908), The production of sound in the drumfishes, the sea robin and the toad-fish. *Ann. N.Y. Acad. Sci.*, **18**, 149–180.
TWERSKY, V. (1951), On the physical basis of the perception of obstacles by the blind. *Amer. J. Psychol.*, **64**, 409–416.
WESTENBERG, J. (1953), Acoustical aspects of some Indonesian fisheries. *J. du Cons.*, **18**, 311–325.
WOHLFAHRT, T. A. (1936), Untersuchungen über das Tonunterscheidungsvermögen der Elritze (*Phoxinus laevis Agass.*). *Z. Vergl. Physiol.*, **26**, 570–604.
WOOD, F. G., Jr. (1954), Underwater sound production and concurrent behaviour of captive porpoises, *Tursiops truncatus* and *Stenella plagiodon*. *Bull. Mar. Sci., Gulf and Caribbean* **3**, 120–133.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 418-425.

Characteristics of the water-masses of the Philippine, Kermadec and Tonga Trenches

By ANTON FR. BRUUN and A. KIILERICH
The *Galathea* Expedition 1950–52, Copenhagen

THE CHIEF purpose of the *Galathea* Expedition 1950–52, The Danish Deep Sea Expedition around the World, was to study the organisms in the deepest parts of the oceans. A considerable number of hydrographic observations, however, were made to learn about the environmental conditions. At least one full series from the surface to the bottom was made in each of the regions where biological work was concentrated. The hydrographic instruments were standard types. During the expedition a total number of 16 reversing thermometers were lost, six of them being simply crushed by pressure at the greater depths in the Philippine Trench.

The greatest care was taken in making observations. Even when only one thermometer was available for each water-bottle, most doubtful temperature readings were repeated. We are therefore fairly confident that our observations, including those presented here, are as exact as any made by specially equipped hydrographic expeditions.

Many technical difficulties resulted from the extreme depth of the Philippine Trench. The effect of high pressure has been mentioned. It was furthermore very difficult to keep the ship exactly above the bottom of the narrow trench, often less than one kilometre wide. We are extremely indebted to Captain S. GREVE, R.D.N. and his officers, for their untiring efforts in fulfilling our requirements. Because of these difficulties we had to repeat the deepest series in the Philippine Trench no less than 10 times, but the efforts were rewarded by 17 observations from depths exceeding 6000 m. The skill and patience of our two assistant hydrographers, Mr. INGOLF CROSSLAND and Mr. ULRIK KLÄNING, is also gratefully acknowledged.

All the observations of the *Galathea* Expedition are to be published in the scientific report of the expedition, but we think it of interest to publish our observations from the Philippine and the Tonga–Kermadec Trenches at once. The first section of the lists of observations (Table I) gives the values observed while the second section (Table II) contains average figures and graphically interpolated figures derived from the total number of reliable observations.

THE PHILIPPINE TRENCH

The temperature from the observations of the *Snellius* Expedition (VAN RIEL, HAMAKER and VAN EYCK, 1950) and the Swedish Deep-Sea Expedition (BRUNEAU, JERLOV and KOCZY, 1953) in the deep water of the trench, are plotted in Fig. 1. The agreement between these and those of the *Galathea* is obvious. The characteristics of the deep water of the trench appears to be very uniform. A minimum of 1·59° C occurs between 3500 and 4000 m. Below this, the temperature increase is very close to that to be expected from adiabatic heating alone. The salinity and amount of oxygen on the other hand are nearly constant for this same interval (Tables I and II).

Thus, it appears that any renewal of the deep water masses of the trench must be derived from that of the West Pacific Basin at the sill depth of the trench (i.e. 3·5–4

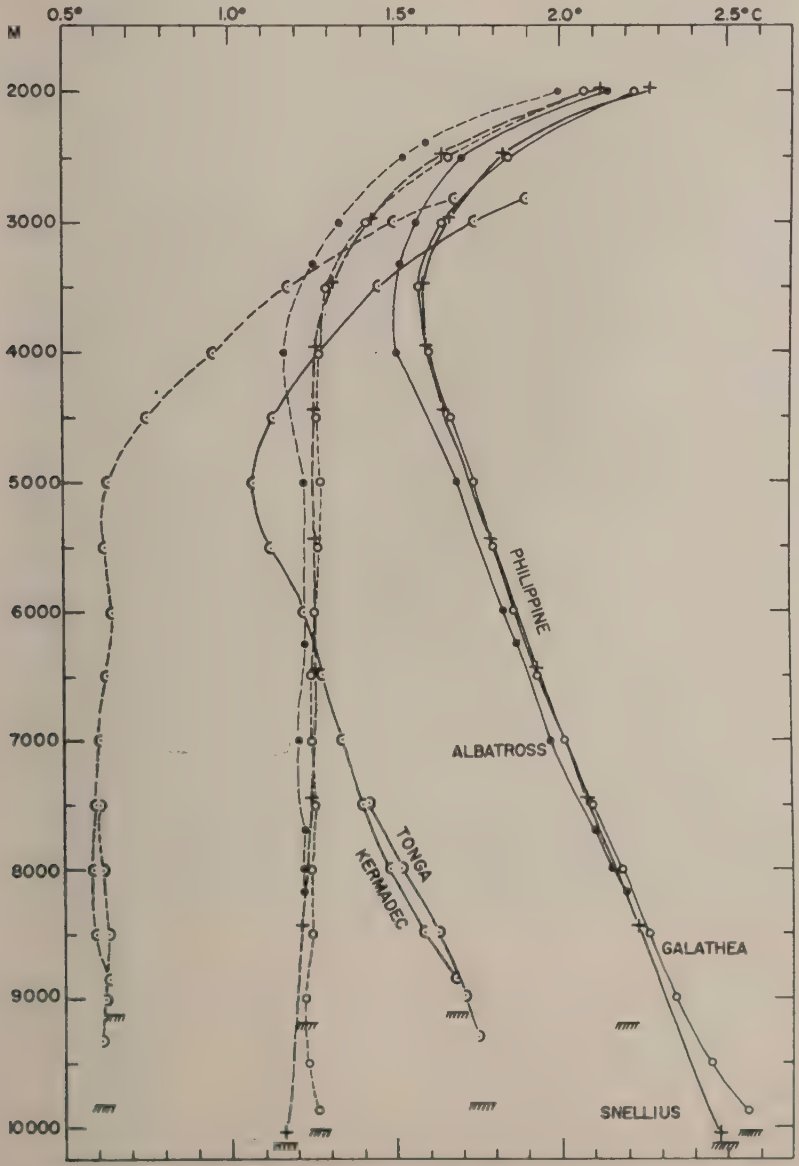

Fig. 1. Temperatures of the Philippine, Tonga, and Kermadec Trenches. Full drawn line indicates temperatures *in situ*, broken line potential temperatures. The signature below each curve denotes the depth at the position of the observations

km) (Fig. 4). This agrees well with the general concept that the Pacific Deep Water is derived from the region south of Australia with roots in the Indian Ocean, and furthermore that there is a slow movement from south to north in the West Pacific.

The velocity of this current is probably so slow that a renewal of the bottom water in the Philippine Trench would require very many years. We know little about the abundance of the organisms in the trenches (BRUUN 1951, 1953 A, B; ZOBELL, 1952; ZENKEVITCH, BIRSCHTEIN and BELJAEV, 1954; ZENKEVITCH, 1955); but in any case they require a certain amount of oxygen. The content of oxygen is relatively high. Therefore, as an additional possibility, acting in the renewal of the trench water, turbidity currents are suggested. The deepest part of the trench (ca. 10000 m) is nowhere more than 90 km distant from the narrow coastal shelf of the Philippines (Fig. 2). Here turbidity currents can easily get started; typhoons will disturb the bottom of the shelf and add to the velocity of the strong tidal currents in the narrow straits of the islands. Eruptions of submarine volcanoes or the frequent earthquakes, which have their epicentres on the western slope (REPETTI, 1931; 199) should also be considered as the cause of bottom sediment slides. The many stones with rounded edges found by *Galathea* must have been carried down in some such way. (Fig. 3); this is also in agreement with SHEPARD (1951).

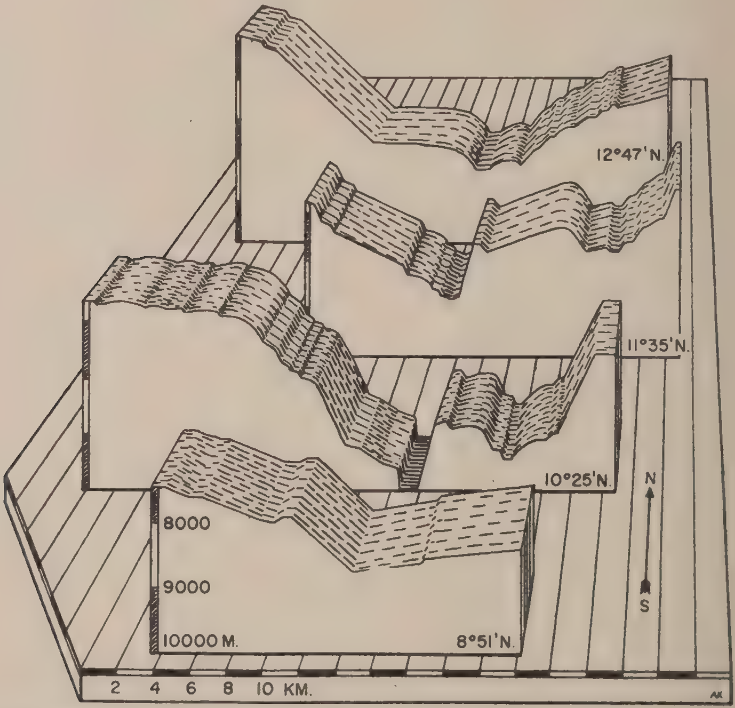

Fig. 2. Four sections of the Philippine Trench. Base line of all sections at 10000 m; distance between any two sections is a little more than 100 km (From KIILERICH, 1953).

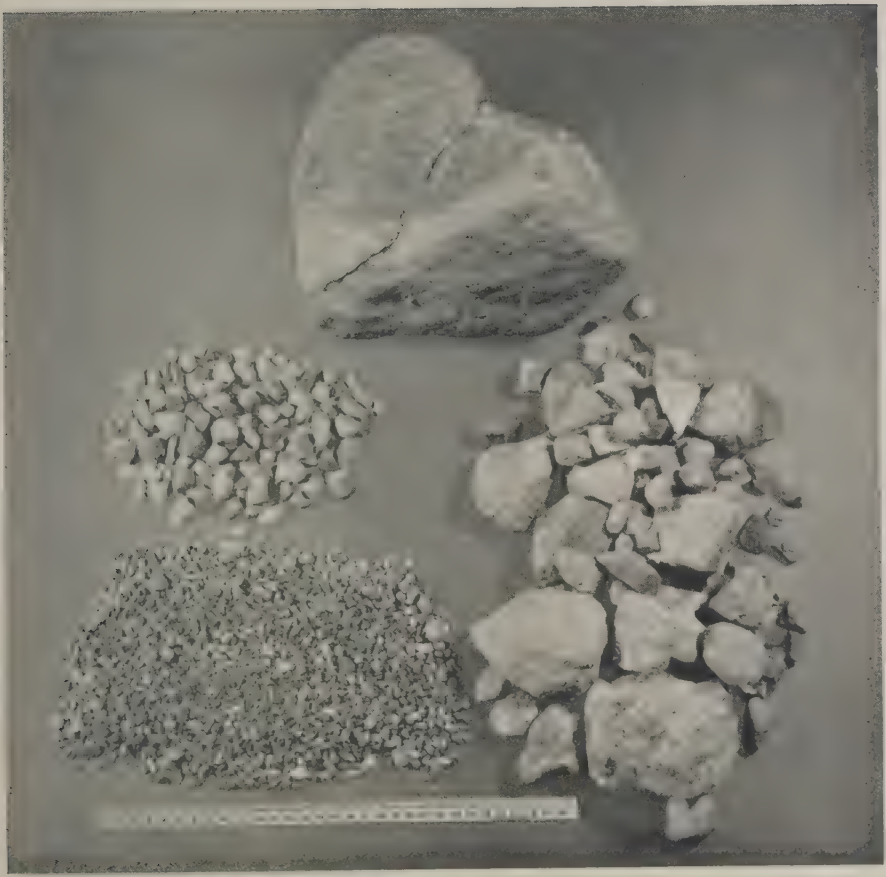

Fig. 3. Stones and gravel brought up by a sledge-trawl from the bottom of the Philippine Trench, 10190 m (From BRUUN, 1953 B).

Such currents of higher density because of suspended particles must bring relatively warm water down, which, after the settlement of the particles, must give rise to thermal convection.

THE TONGA–KERMADEC TRENCHES

The water of the greater depths of the Tonga-Kermadec Trenches differs in several ways from that of the Philippine Trench. This is to be expected from the geographical position, which is much closer to the sources of the bottom water of the Pacific. This is shown by the minimum temperature, 1·07° C, at about 5000 m (see Figs. 1 and 4). Here also the increase in temperature towards the bottom closely follows what would be expected from adiabatic heating.

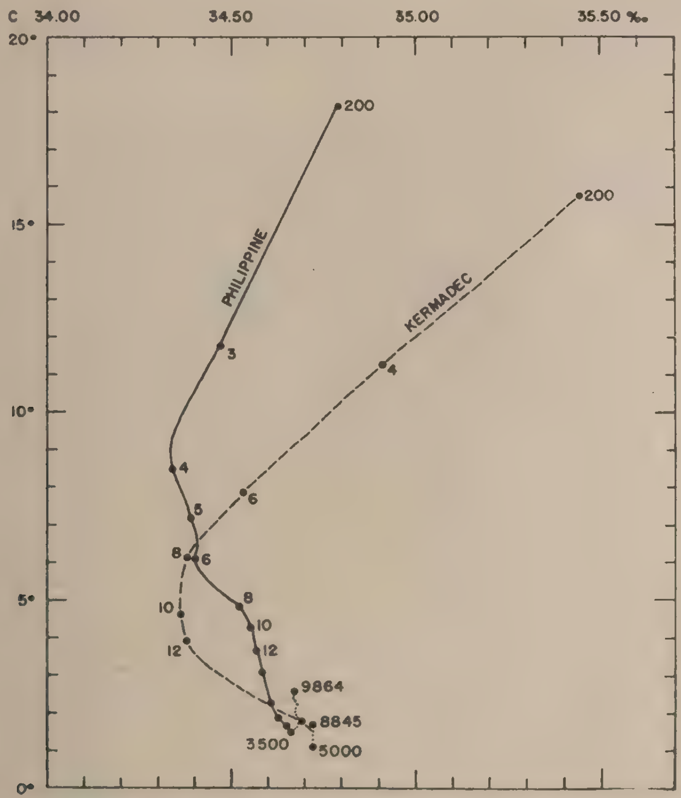

Fig. 4. T–S diagram of the water masses of the Philippine and Kermadec Trenches. Except for the uppermost and lowermost observations the figures along the curves denote hundreds of m.

Galathea Station nr. 686 was taken in the Tonga Trench, 8 degrees of latitude north of the full series of observations of St. 677 in the Kermadec Trench. Lack of time prevented us from making more than three observations, but they are sufficient to prove that the deep water is essentially the same. This corroborates well the results from the echo-soundings, that the connection between these trenches is below the level of the surrounding basin. Lengthwise of the connection we found no depth shallower than 6000 m. Therefore it might even be reasonable to speak of one trench only, the Tonga-Kermadec Trench. The potential temperatures calculated are as constant as could be expected from the quality of thermometers, just as in the Philippine Trench. We want, however, to draw attention to the slight increase close to the bottom. It is only 0·04° C, but it has been recorded on four occasions with two different thermometers. This is the opposite of what was found by the *Snellius* Expedition (VAN RIEL, *et al.*, 1950, 29–30); it will be most important to have this disagreement further studied. As it is, it does not justify further comment.

Table I

Values of temperature, salinity, density and oxygen at various depths as actually observed by the Galathea

St. 412. Philippine Trench. 11° 13′ N. 126° 21′ E. 12–13/7 1951

Depth 8981–8956 *m*

m	*C*°	*S*‰	σ_t	O_2 *ml/L*
0	29·60	34·20	21·46	—
24	·15	·15	·41	4·38
47	·00	·28	·54	·41
71	28·70	·43	·76	·36
94	·38	·58	·97	·50
142	23·42	35·00	23·83	3·94
189	18·78	34·83	24·98	·55
283	12·44	·49	26·13	2·71
378	8·94	·33	·65	·10
472	7·55	·39	·92	1·62
567	6·40	·39	27·07	·67
756	5·00	·51	·34	·80
945	4·45	·55	·43	2·17
1133	3·77	·56	·50	·06
1417	·26	·58	·57	·20
1890	2·33	·60	·67	·39
2362	1·93	·62	·71	·66
2835	·72	·64	·74	·96
3307	·59	·66	·76	3·38
3779	·59	—	—	—
4252	·63	·67	·77	·08
4724	·71	·68	·77	·32
5669	·81	·68	·76	2·92
6755	·95	·66	·74	·26
7700	—	·66	—	3·13
8076	2·22	·68	·73	·22
8503	—	·66	—	·06

St. 430. Philippine Trench. 10° 20′ N. 126° 37′ E. 3–4/8 1951

Depth 10110 *m*

m	*C*°	*S*‰	σ_t	O_2 *ml/L*
945	4·82 (*a*)	34·51	27·36	1·16
1606	2·99	·58	·59	·62
2079	·16	·61	·69	·92
7640	·12	—	—	—

St. 431. Philippine Trench. 10° 21′ N. 126° 38′ E. 4–5/8 1951

Depth 10110 *m*

m	*C°*	*S°/oo*	σ_t	O_2 *ml/L*
7558	2·01 (*a*)	34·69	27·75	3·04
8503	·27	·69	·73	·11
9165	·35	·67	·72	2·88
9636	·50	·67	·71	3·27

St. 433. Philippine Trench. 9° 51′ N. 126° 51′ E. 5–6/8 1951

Depth 10003 *m*

m	*C°*	*S°/oo*	σ_t	O_2 *ml/L*
3779	1·57	34·67	27·77	3·27
4252	·57 (*a*)	·69	·78	·15
4724	·70	·67	·77	·11
5669	·80	·69	·77	·12
6614	·95	·69	·76	·36
7511	·97 (*a*)	·68	·75	·20
8456	2·18	·66	·72	·16
9498	·28 (*a*)	·66	·71	2·93
9589	·47	·69	·72	3·31

(*a*) Thermometer not absolutely reliable.

St. 440. Philippine Trench. 10° 25′ N. 126° 40′ E. 14/8 1951

Depth 10016 *m*

m	*C°*	*S°/oo*	σ_t	O_2 *ml/L*
3068	1·61	34·65	27·75	2·92
5900	·83	·67	·75	3·01
7788	2·13	·68	·74	2·90
9770	·56	·67	·70	3·19
9864	·55	·67	·70	·11

St. 677. Kermadec Trench. 28° 38′ S. 175° 53′ W. 4–5/3 1952

Depth 9127–9192 *m*

m	*C°*	*S°/oo*	σ_t	O_2 *ml/L*
0	24·02	35·64	24·14	—
47	*C* 22·	·58	·68	5·15
94	17·92	·55	25·74	·02
182	16·08	·46	26·10	4·55
376	11·77	34·97	·63	·35
564	8·25	·58	·93	·61
766	6·42	·39	27·03	·97
956	5·13	·37	·18	·50
1145	4·07	·37	·30	·16
2822	1·89	·68	·74	3·37
3762	·34	·72	·83	4·44
4232	·19	·72	·83	·52
4723	·09	·72	·84	·58
5194	·07	·72	·84	·48
5665	·16	·70	·83	·56
6496	·27	·72	·82	·62
7905	·46	·70	·81	·60
8845	·68	·72	·81	·56

St. 686. Tonga Trench. 20° 53′ S. 173° 51′ W. 11/3 1952

Depth 9818 m

m	*C°*	$S^\circ/_{oo}$	σ_t	O_2 *ml/L*
7428	1·40	34·71	27·81	4·52
8373	·60	·71	·80	·46
9318	·74	·71	·79	·48

Table II

Average values of temperature, salinity, density and oxygen at standard depths as derived from interpolation on graphs and based on the total number of reliable observations

Philippine Trench. Interpolation referred to standard depths; based on all *Galathea* observations

m	*C°*	$S^\circ/_{oo}$	σ_t	O_2 *ml/L*	*potential temp.*
0	29·40	34·20	21·46	—	
25	·14	·15	·40	4·4	
50	28·97	·30	·57	·4	
75	·65	·46	·79	·4	
100	·10	·63	22·11	·5	
150	22·65	·99	24·04	3·9	
200	18·15	·79	25·09	·5	
300	11·75	·47	26·24	2·7	
400	8·50	·34	·74	·0	
500	7·12	·39	·98	1·6	
600	6·05	·40	27·12	·7	
800	4·86	·52	·36	·9	
1000	·22	·55	·46	2·1	
1200	3·62	·57	·53	·1	
1500	·05	·59	·59	·2	
2000	2·22	·61	·68	·4	2·07
2500	1·84	·63	·72	·6	1·66
3000	·64	·65	·75	·9	·41
3500	·57	·67	·77	3·3	·29
4000	·60	·67	·77	·2	·27
4500	·66	·68	·77	·1	·26
5000	·73	·68	·77	·1	·27
5500	·79	·69	·76	·0	·26
6000	·85	·69	·76	·0	·25
6500	·92	·68	·75	·0	·24
7000	2·00	·68	·75	2·3	·24
7500	·09	·67	·74	3·0	·25
8000	·18	·68	·73	·0	·24
8500	·26	·68	·73	1·1	·24
9000	·34	·67	·72	·0	·22
9500	·45	·67	·71	2·9	·23
9864	·56	·67	·70	3·1	·26

St. 677. Kermadec Trench. Interpolation referred to standard depths. 28° 38′ S. 175° 53′ W. 4–5/3 1952

m	*C°*	*S°/₀₀*	σ_t	O_2 *ml/L*	*potential temp.*
0	24·02	35·64	24·14	—	
50	*C* 22·	·58	·68	5·2	
100	17·80	·54	25·76	·0	
200	15·75	·44	26·16	4·5	
400	11·30	34·91	·68	·4	
600	7·90	·53	·98	·6	
800	6·15	·38	27·10	5·0	
1000	4·65	·36	·25	4·4	
1200	3·95	·38	·34	·1	
3000	1·74	·69	·77	3·5	1·51
3500	·45	·72	·82	4·3	·18
4000	·27	·72	·83	·5	0·95
4500	·13	·72	·84	·5	0·75
5000	·07	·72	·84	·5	0·63
5500	·12	·72	·84	·5	0·62
6000	·22	·72	·83	·6	0·64
6500	·27	·72	·83	·6	0·62
7000	·33	·72	·83	·6	0·60
7500	·40	·72	·82	·6	0·59
8000	·48	·72	·82	·6	0·58
8500	·58	·72	·81	·6	0·59
8845	·68	·72	·81	·6	0·63

St. 686. Tonga Trench. Interpolation referred to standard depths. 20° 53′ S. 173° 51′ W. 11/3 1952

m	*C°*	*S°/₀₀*	σ_t	O_2 *ml/L*	*potential temp.*
7500	1·41	34·71	27·81	4·5	0·60
8000	·51	·71	·80	·5	0·61
8500	·62	·71	·80	·5	0·63
9000	·70	·71	·79	·5	0·62
9318	·74	·71	·79	·5	0·61

REFERENCES

Bruneau, L., Jerlov, N. G. and Koczy, F. F. (1953), Physical and chemical methods. *Repts. Swedish Deep-Sea Exped.*, 1947–1948, *Phys. Chem.*, **3** (4), 101–112.

Bruun, A. Fr. (1951), The Philippine Trench and its bottom fauna. *Nature*, **168**, 692.

Bruun, A. Fr. (1953 a), Problems of life in the deepest deep sea. *Geogr. Mag.*, **26**, 247–262.

Bruun, A. Fr. (1953 b), Dybhavets Dyreliv. In: A. F. Bruun, Sv. Greve, H. Mielche and R. Spärck, *Galatheas Jordomsejling*, 1950–52, 153–192.

Kiilerich, A. (1953), Ekkolod og hydrografiske Undersøgelser. In: A. F. Bruun, Sv. Greve, H. Mielche, R. Spärck, *Galatheas Jordomsejling*, 1950–52, 43–54.

Repetti, Wm. C. (1931), Philippine earthquakes. Marine epicenters. *Publ. Manila Observ.*, 3 (9), 199–203.

Shepard, F. P. (1951), Transportation of sand into deep water. *Soc. Economic Paleontol. Mineral., Spec. Publ.*, **2**, 53–65.

Van Riel, P. M., Hamaker, H. C. and van Eyck, L. (1950), Tables, serial and bottom observations, temperature, salinity and density. *Snellius Exped., Oceanogr. Res.*, 1929–1930, 2 (6), 44 pp.

Zenkevitch, L. A. (1955), Erforschungen der Tiefseefauna im Nordwestlichen Teil des Stillen Ozeans. *Int. Union Biol. Sci.*, (B), **16**, 72–84.

Zenkevitch, L. A., Birschtejn, J. A. and Beljaev, G. M. (1954), Izutchenie fauni Kurilo-Kamtchatskoj viadinui. (The exploration of the fauna in Kurile-Kamtchatka Deep). *Priroda*, 1954, 61–73.

Zobell, C. E. (1952), Bacterial life at the bottom of the Philippine Trench. *Science*, **115**, 507–508.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 426-434.

Polarization of scattered sunlight in deep water*

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Summary—1. Photographic measurements of the polarization pattern of underwater illumination were made at depths of 30, 60, 100, 150, and 200 m in oceanic water with a vertical extinction coefficient corresponding to Secchi disc readings between 22–26 m. A special polarization analyzer, attached to the outside of a deep-sea camera case, provided in a single photograph direct evidence for: (a) presence or absence of polarization with a high degree of sensitivity; (b) type of polarization; (c) plane of polarization, if linear; (d) rough comparative indication of the degree of polarization. By photographing the interference pattern formed by this analyzer when traversed by polarized light, records of the polarization of horizontally scattered sunlight were obtained in four azimuths relative to the sun's bearing: 0°, 90°, 180°, 270°, at eleven different stations, including two at each depth except 200 m.

2. Horizontally scattered light was found to be polarized at all depths, 200 m included, and in all directions tested; the type of polarization was linear in every instance. In so far as could be judged from the photographs (Fig. 3), the percentage polarization at 200 m appeared to be at least as great as at lesser depths.

3. The plane of polarization was always horizontal in lines of sight toward and away from the sun's bearing but was tilted toward the sun in azimuth's normal to these; this effect of the sun's position was still considerable at 200 m. The amount of tilting occurring in lines of sight 90° from the sun's bearing was primarily related to the angle of refraction for sunlight at the air–water interface (Fig. 2), but a second effect, resulting from depth of light penetration, was shown by the decrease in the tilting of the polarization plane as depth was increased.

4. It is concluded that: (a) scattered sunlight underwater is linearly polarized to considerable depths, probably throughout the photic zone; (b) the pattern of polarization is dependent on the sun's position at least to a depth of 200 m and (c) such optical phenomena therefore may be important in the behaviour of photic zone bathypelagic animals as well as epipelagic forms.

INTRODUCTION

PREVIOUS MEASUREMENTS (WATERMAN, 1954 A) have shown that natural underwater illumination is linearly polarized in patterns which seem basically similar to those of the blue sky.† This is true of the upper 15 m or so of water to which the earlier work was limited. Since the most probable origin for this polarization would appear to be the molecular or fine particle scattering of directional light rays penetrating the water, it was predicted that linear polarization of submarine illumination should occur as deep as significant amounts of directional light are transmitted. It was also indicated that, since certain terrestrial and shallow water animals are known to be capable of utilizing polarized light in the sky for their orientation and navigation, underwater polarization may prove to be a factor of considerable ecological importance in the location and migration of animals of the whole photic zone. For these reasons the extension of our knowledge of submarine polarized light into deep water is a matter relevant to several points of interest.

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* Contribution No. 763, Woods Hole Oceanographic Institution.

† This introductory statement refers only to polarization arising within the water itself. It does not include the direct underwater observation or measurement of polarized sky light. The known relation between these two sources of polarization has previously been described for shallow water (WATERMAN, 1954 A). Further measurements will be required to establish in deeper water the effective penetration and influence of polarized sky light, as opposed to direct sunlight, which is unpolarized in the atmosphere.

The present report describes the results of photographic polarization measurements down to 200 m which extend our information to depths in excess of ten times those previously studied. It clearly proves that polarization of sunlight under water is not merely a superficial phenomenon but one which also must be reckoned with at considerable depths.

ACKNOWLEDGEMENTS

The author is greatly indebted to a number of people who helped him in many ways while preparing for and executing these measurements. Particular mention should be made of various Staff members of the Woods Hole Oceanographic Institution and the Officers and Crew of R.V. *Atlantis*: Dr. C. O'D. Iselin, Mr. David Owen, Mr. Richard Edwards, Mr. Lloyd Hoadley, Mr. Valentine Worthington and Captain Scott Bray. Hearty thanks are also due to Miss Virginia Withington, Mr. Charles Robinson and Mr. Wallace Phelps of the Edwards Street Laboratory at Yale University.

EQUIPMENT AND PROCEDURE

The data reported here were obtained in the southwest North Atlantic just west and northwest of Bridgetown, Barbados, B.W.I. (13° N, 59° W) working from R.V. *Atlantis*. Polarization measurements were made at 30, 60, 100, 150 and 200 m. The average echo-sounding depth at the various stations was about 1,200 m so that no effect of reflection or light scattering by the bottom could reasonably have influenced the results.

Secchi disc readings ranged from 22–26 m, indicating moderately clear oceanic water in the upper layers. These depths correspond to vertical extinction coefficients of about 0·055–0·065 (Clarke, 1941), or to overall transparency between Jerlov's (1951) types I and II oceanic water. The sea was moderate (Beaufort 2–3), confused and occasionally had a large swell during the work.

While the measurements were being made, the sun was shining on the sea surface in all cases, although as work progressed on the 200 m station (No. 11), a high thin overcast slowly cut down the direct sunlight from full to a point where shadows were just visible. In all other cases the sky was either mainly clear overhead or nearly completely clear. Stations were made at various sun's altitudes from 26–52°. The latter was close to the local noon maximum for the period around December 1 when this work was done.

In order that the results obtained may be effectively presented, the optical equipment used and the procedure for making the measurements will first be described.

The basic units of equipment employed were (1) a special polarization analyzer and (2) a camera. The latter was arranged to record the interference figure produced by the analyzer when it was traversed by polarized light. This analyzer, which has been used before for visual observations (Waterman, 1954 a) is made up of two essential optic components. The first of these is a calcite crystal about 3·5 mm thick cut at right angles to its optic axis; the second is a circular polarization analyzer. This consists of a quarter wave plate and a linear polarizer in that order with the slow axis of the former oriented 45° clockwise from the transmitting axis of the latter.

When convergent polarized light passes through this optic system, an interference pattern is formed. Four parameters of the pattern are directly dependent on the properties of the light traversing the analyzer. The figure's contrast and extent depend roughly on the intensity and percent polarization of the incident light. Its colour is related to the wavelengths transmitted. Finally, the geometry of the interference figure varies with different kinds of polarized light whether linear, elliptical or circular.

Such patterns arise because light rays in the convergent beam which pass through the crystal plate obliquely, i.e., not parallel to its optic axis, will be split up into two rays by the calcite's birefringence. These undergo different retardations in passing through the crystal. On emerging from it and traversing the circular analyzer, they form areas of cancellation and reinforcement in a radially symmetrical pattern whose relative size depends on the thickness and birefringence of the crystal.

With monochromatic polarized light the interference pattern consists of alternating dark and light concentric rings, successive light areas of the pattern corresponding to differences of one wave-length in the oblique ray paths through the calcite. With white light a series of brilliant interference colours in isochromatic rings will be added to this basic pattern.

If the light entering the analyzer is circularly polarized, the interference figure obtained under the conditions specified will be a series of complete circular isochromatic curves, starting from a white centre spot and becoming closer and closer together in the higher order rings (Fig. 1A). With elliptically polarized light these rings are distorted into a series of ellipses.

The interference figure produced by linearly polarized light is broken up into four quadrants at the limits of which the isochromatic rings are interrupted and displaced radially. In two diametric quadrants the arcs are moved outward and two dark spots appear in their central sectors (Fig. 1B); in the other sectors the arcs are displaced inward and the centre remains white.

The breaks in the concentric rings are parallel to the *e* and *h* vectors of the linearly polarized incident light. With a negative analyzer crystal, like calcite, and the circular analyzer axes set as described, the *e* vector will be parallel to the breaks which delimit the clockwise edges of the two dark centre sectors.

It should be emphasized that this type of analyzer, although simple, has several important advantages in an application like the present one. Unlike any other polarization analyzer, the present device provides the maximum information of which it is capable without the need of rotating it or moving any of its parts. The plane of linearly polarized light can be observed directly by inspection regardless of the angular relation between the plane of the incident light and the axes of the conjoined quarter wave plate and the linear polarizer.

This is true only when the latter two units are oriented relative to each other as specified. If their axes are not aligned at 45°, or if only a linear analyzer is used with the calcite crystal, the interference figure will change with the rotation of the analyzer. As this happens, a dark cross-like isogyre will be superimposed on the isochromatic lines. Its position and intensity will depend on the relation of the analyzer axis to the plane of incident light polarization. Hence the *e* vector cannot be recognized directly by inspection without rotating the instrument.

Another important property of the analyzer described lies in its high sensitivity. Small percentages of polarization of the order of 5% may readily be detected. The instrument has, therefore, proved useful in addition to its present application in monitoring the illumination of experimental apparatus where polarization of the light source or stray polarized light in the system had to be avoided (WATERMAN, 1950; 1954 B).

It is of interest that, although interference patterns provide a standard means of structural analysis in crystallography, their application in the present instance reverses the known and unknown factors in the optical parameters. In the measurements here described it is not the crystal plate whose characteristics are to be determined but rather the polarization of the deep-sea illumination which traverses it.

A further convenient property of the polarization analyzer used is the fact that the interference figure is optically located at infinity. Consequently the instrument may be fastened directly over the lens of a camera focussed at its principle focus and a record obtained which indicates whether or not polarized light is present or not, even in small amounts. Its type and plane, if it is linearly polarized, will likewise be recorded with precision.

A complication is introduced for deep-sea work, however, by the need for enclosing the camera in a water-proof case whose window is almost certain to exhibit strain birefringence when subjected to pressure. Such an effect was actually observed in some preliminary photographs taken at about 30 m depth with a hand-held camera.*

In that instance the camera with the analyzer attached over the lens was protected in a transparent plastic box. This was apparently birefringent when the pictures were taken since the figure recorded showed elliptical polarization in the horizontal light pattern. Such has never been observed visually under water in level lines of sight (WATERMAN, 1954 A) nor was it ever found in deep water photographs where the possibility of strain birefringence had been eliminated.

To obviate this difficulty in the present instance the analyzer was mounted outside the pressure case enclosing the camera. Both front and back of the optical sandwich involved were thus exposed to equal pressures. No detectable effect of the hydrostatic pressure itself (about 20 atmospheres at the deepest station) was ever observed. Of course, any strain birefringence arising in the window through which the camera looked out of its case would have no effect in this situation since it occurred between the analyzer and the lens.

The camera employed was a 35 mm Robot with an f/2·8 Zeiss tessar lens. It was arranged to be triggered by a solenoid controlled from the ship. After each exposure the film was automatically advanced by the camera mechanism so that 15–20 pictures could be taken on a single lowering of the apparatus. The Robot was mounted in a Ewing-type deep-sea camera case sealed with an O-ring. The lens was aligned with a plane glass window outside of which the polarization analyzer was attached as already described. A two-conductor insulated cable ran from the solenoid operating the camera shutter to the deck laboratory of *Atlantis* where the exposures were controlled.

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* The author is much indebted to Mr. CONRAD LIMBAUGH and Mr. GEORGE SHUMWAY of the University of California for their assistance in taking these underwater photographs at La Jolla.

The whole deep-sea camera and case were mounted on a weighted frame suspended from the end of the ship's hydrographic cable. When the equipment was lowered into the water, the camera lens and interference analyzer were quite accurately directed horizontally. This was so even while the ship was steaming ahead at slow speeds, a fact which was checked by diving with the ship under way. Consequently the frame of the photographic negatives has been taken as the vertical and horizontal reference for analysis of the data.

Previous work (WATERMAN, 1954 A) had shown that the intensity and plane of the polarization of underwater illumination were dependent on the relation between the line of sight and the bearing of the sun. Consequently, it was important for the present deep-water measurements to control the azimuth in which the pictures of the polarization pattern were taken. To do so a large fin of sheet aluminum was attached to the frame holding the camera in such a way that the horizontal direction in which the camera would point coincided with the ship's heading.

The procedure used in obtaining the photographic data was as follows. The camera, loaded with Eastman Kodak Tri-X film, which has an American Standards Exposure Index of 200, was lowered to the depth desired. Then the ship steamed slowly ahead in the sun's azimuth, a manoeuvre which would shortly bring the camera's direction of view into alignment with the sun's bearing. After a period which experience with the resulting negatives showed was adequate for the slowly towed camera to settle into this orientation, a series of three exposures was made separated by 5 second intervals.

Exposure times and diaphragm stops were first set on the basis of the estimated extinction coefficients of the water mass concerned, then, if necessary, corrected from experience. No photometric transparency measurements were made, but an approximate value was obtained for the surface layers by the use of the Secchi disc at each station (CLARKE, 1941) and by comparison with published data from stations made in nearby areas (JERLOV, 1951). Actual exposures used varied with the sun's altitude as well as depth of the camera from 1/25 sec at f/4 for 30 m to 20 sec at f/2·8 for 200 m.

After pictures had been taken in one direction, the ship's course was altered 90° clockwise, and after a suitable wait of about 5–10 min for the camera and cable to swing around, another three photographs were made, this time looking 90° to the right of the sun's azimuth. Similarly two more sets of exposures were made in directions 180° and 270° to the right of the sun's bearing.

It should be mentioned that because of the wind (force 3–4 Beaufort) and sea running at the various stations, it was not always possible to obtain records under ideal conditions for each of the four azimuths tested. In some cases the wire angle instead of being negligible was appreciable, particularly for downwind or crosswind legs of the station. Similarly the behvaiour of the cable after a turn sometimes showed that the apparatus was slow in aligning its heading with that of the ship. Reasonable compromises between ideal recording conditions and practical handling circumstances of the ship and gear had therefore to be made.

In the absence of a more elaborate apparatus where the camera's direction could be immediately and accurately controlled from the surface and monitored with repeating compass and precise vertical reference, the reliability of the present results could be insured only by the care and experience exercised in carrying out the manoeuvres described. It could be checked, however, by the consistency of the data obtained, both internally and with reference to relations indicated by previous shallow-water observations.

A total of 11 stations were made. Of these the first 4 and No. 6 showed considerable internal inconsistencies for azimuth, apparently arising from inexperience with difficulties like those outlined. But on the basis of their coherence, the data for the remaining 6 stations indicate that such interference had been minimized. These include one set of records each at 30, 60, 100, 200 m and two at 150 m.

RESULTS

The data of these measurements provide information relevant to four or five different aspects of the general problem.

In the first place every photograph taken during the present deep-water series showed a well-developed interference figure (Figs. 2, 3). This proved that the scattered horizontal underwater illumination in the directions photographed was polarized at all depths tested including the deepest, 200 m. Furthermore, as the interference pattern clearly consisted of four quadrants of isochromatic curves made up of broken concentric rings with two diametrically opposite dark central sectors, this light must have been linearly polarized.

Table I

Station No. 9 13° 08′ N, 59° 50·5′ W. Dec. 2, 1954
Sun's altitude: 34° 40′ Sun's azimuth: 129°
Angle of sunlight incidence: 55° Calculated angle of refraction: 38°
Depth of measurements: 60 m Depth to bottom: 1150 m

Direction relative to sun's bearing	0°	90°	180°	270°
Tilt of polarization plane				
Exposure ♯1	0°	17° left	1·5° left	11° right
♯2	1° right	19° left	2·0° left	16° right
♯3	0°	—	2·0° left	19° right
Average	0·3° right	18° left	1·8° left	15·3° right

Although the method of polarized light analysis employed does not permit any close estimate of percentage polarization, there is some evidence pertinent to this matter in the photographs. In so far as it can be gauged by the intensity and extent of the interference pattern photographed, the degree of light polarization at 200 m seemed to be about as great as at any shallower depths. The number of concentric isochromatic rings recorded at this deepest station is fully as large as at any other in the present series.

Also it is clear from the same kind of evidence that in deeper water there is no marked change in percent polarization with direction of view relative to the sun's azimuth. In fact No. 8 at 30 m (Fig. 2) was the only station obviously providing evidence for this relation which was always found visually in shallow water (WATERMAN, 1954 A).

On the other hand, the effect of the relative bearing of the sun on the plane of polarization was a prominent and highly significant feature of the records at all stations. This is exemplified by the data for stations 9 and 11 which are presented in Tables I and II and by Figs. 2 and 3 for stations 8 and 11.

In general the *e* vector of the polarization was horizontal in the sun's and the anti-sun's bearings but was tilted towards the sun at azimuths normal to these lines of sight. When the polarization plane appeared to be tilted in bearings towards or away from the sun, it has been assumed that this was the result of the camera not being precisely horizontal or pointing accurately along the ship's heading as discussed under procedure. The magnitude of these influences, obvious in the directions cited, should in addition give some information on the reliability of the measurements made normal to the sun's azimuth where the present data do not otherwise provide any estimate of variance.

The tables and photographs illustrate two important points inherent in the total data. First is that the sun's position influenced the pattern of submarine polarization at all depths so far studied, including 200 m, the deepest of the present stations, and the shallow water observations made previously. The optical effects involved here were (1) the angle of refraction of the incident rays of sunlight and (2) the apparent origin of underwater polarization from primary Rayleigh scattering of directional light beams, which causes the polarization plane to be normal to the angle of refraction.

Table II

Station No. 11 13° 07′ N, 59° 53′ W. Dec. 2, 1954
Sun's altitude: 51° 40′
Sun's azimuth: 201°
Angle of sunlight incidence: 38°
Calculated angle of refraction: 27°
Depth of measurements: 200 m
Depth to bottom: ——

Direction relative to sun's bearing	0°	90°	180°	270°
Tilt of polarization plane				
Exposure ♯1	0°	7·5° left	0°	11° right
♯2	0·5° left	7·5° left	0°	7·5° right
♯3	1° left	7·0° left	—	8·5° right
Average	0·5° left	7·3° left	0°	9·0° right

This effect was certainly predominant in shallow water. It was also at the 30 m station (No. 8) in the present series (Fig. 2). Here the tilt of the polarization plane averaged 43° for lines of sight normal to the sun's bearing. This angle was almost identical with the corresponding angle of refraction (42°) calculated from the observed solar altitude, assuming a refractive index for the water of 1·34.

Such an effect of the sun's altitude, and hence the angle of refraction of sunlight entering the water, must also be involved in the plane of polarization at greater depths, too. Yet the present data do not afford much direct evidence for this since repeated measurements were not made systematically at the same depth with different solar altitudes. However, in the single satisfactory case where such a comparison can be made, strong support for this generalization is found. This comes from the data of stations 7 and 10, both at 150 m.

Here the angles of refraction of sunlight, computed from the sun's elevations, were not the same because of the different times of day when the two sets of photographs were made. It will be seen in Table III that the deviations of the polarization planes

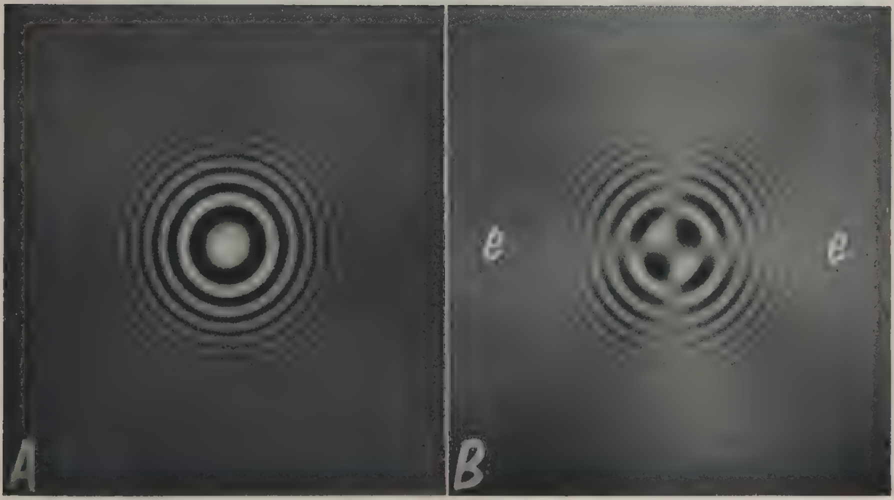

Fig. 1. Interference patterns formed by the analyzer when traversed by polarized light. *A*. Figure produced by circularly polarized light having a counterclockwise rotation; if its rotation were clockwise, the pattern would have a dark centre instead of a light one. *B*. Figure observed with linearly polarized light produced by a type H Polaroid filter. The interruptions in the isochromatic rings are parallel to the electric and magnetic vectors of the incident light. The plane of the *e* vector is horizontal, as labelled, and coincides with the clockwise edge of the dark central sectors.

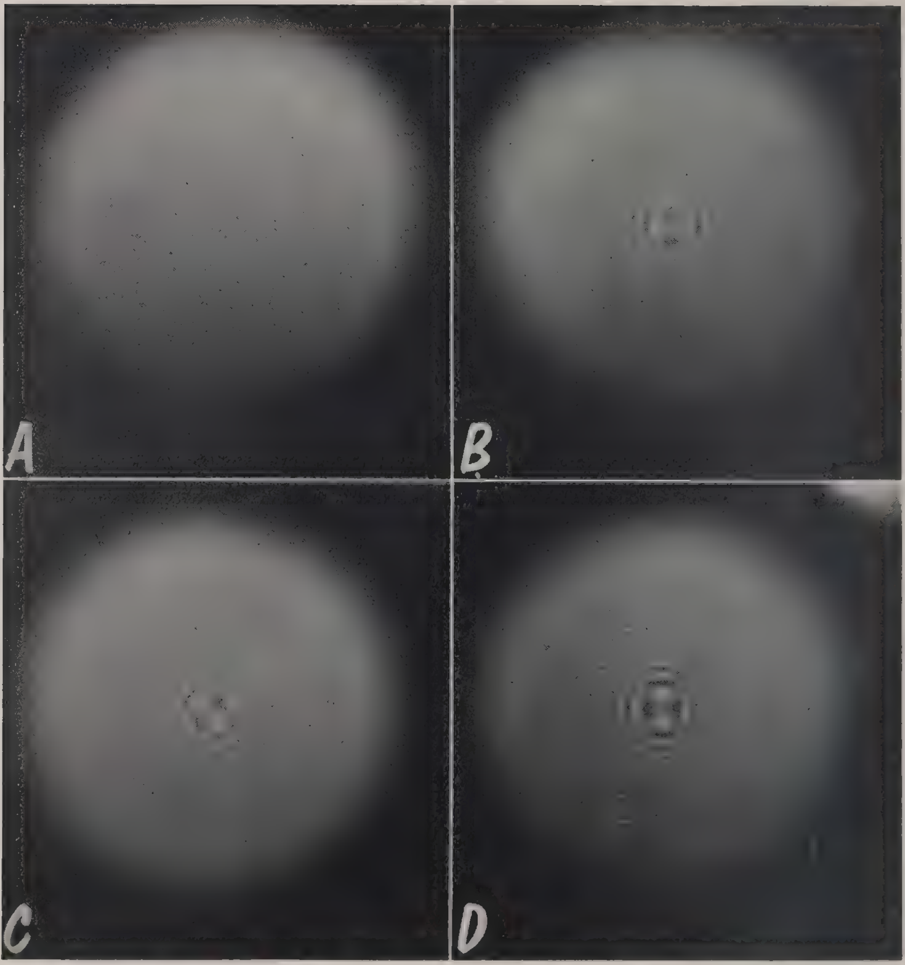

Fig. 2. Interference patterns formed by natural light underwater at 30 m depth (station 8). The analyzer and camera were directed horizontally in azimuths of (*A*) 0°, (*B*) 90°, (*C*) 180°, and (*D*) 270° relative to the sun's bearing. The scattered sunlight is seen to be linearly polarized in all cases, with the polarization apparently weakest at 0° (*A*) and stronger particularly at 90° (*B*) and 270° (*D*). The planes of polarization (angles between plane of light vibration relative to the horizontal) measured in uncropped prints where the film frames provide the vertical and horizontal references were: (*A*) 8·5° tilt toward the right, (*B*) 42·5° left, (*C*) 4° right and (*D*) 43° right. Exposures: ½ sec, f/4, Tri-X film. Sun's altitude 26°.

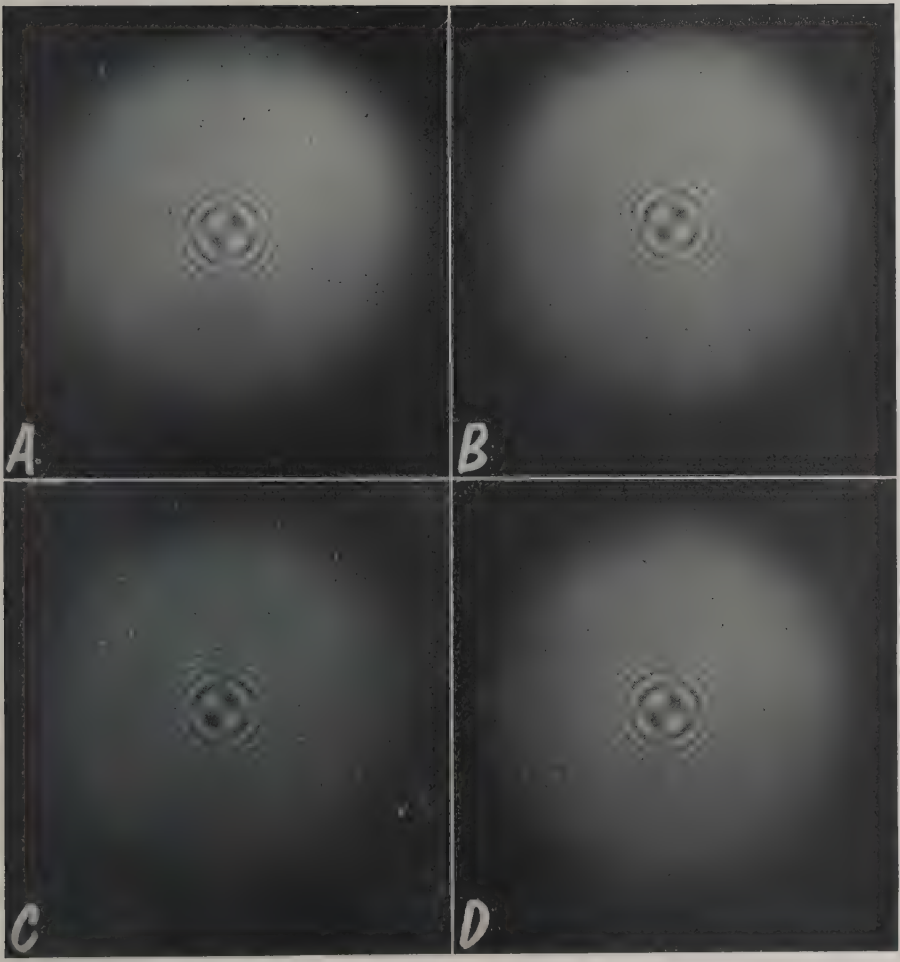

Fig. 3. Interference patterns formed by natural light underwater at 200 m depth (station 11; for the complete protocol see Table II). The analyzer and camera were directed horizontally in azimuths of (*A*) 0°, (*B*) 90°, (*C*) 180° and (*D*) 270° relative to the sun's bearing. The scattered sunlight is seen to be linearly polarized in all cases with the polarization apparently of comparable intensities in all directions. Implied by the extent and contrast of the pattern is the fact that polarization is still considerable even at this depth. The planes of polarization (angles between the planes of light vibration and the horizontal) measured in uncropped prints where the film frames provide the vertical and horizontal references were: (*A*) 0·5° tilt toward the left (*B*) 7·5° left, (*C*) 0° (no tilt) and (*D*) 8·5° right. Exposures: 20 sec, f 2·8, Tri-X film. Sun's altitude 52°.

from horizontal were correspondingly different even though they do not agree numerically with the angles of refraction. Note, however, that the ratios of the observed angles to the calculated ones were more nearly alike. In other words, the observed angles of polarization deviated significantly from those calculated simply on the basis of surface refraction. This introduces the second point illustrated by Tables I, II, and Figs. 2, 3.

The second point is the effect of depth *per se* on the tilt of the polarization plane independent of the solar altitude. This influence was obvious in the data of all the stations deeper than 30 m. At 200 m (Table II), for example, the average tilt of the polarization plane 90° from the sun's azimuth was 8°, which was only 30% of the angle of refraction of the sunlight at the surface when the photographs were made. For the stations at intermediate depths, the tilt of the polarization plane was also intermediate, being significantly less than the angle of refraction yet considerably larger than the tilt found at 200 m.

Table III

Station	*Sun's altitude*	*Calculated angle of refraction* (*r*)	*Polarization tilt* (*p*)	*p*/*r*%
7	30°	40°	15·5°	39%
10	52°	27°	11·6°	43%

DISCUSSION

The new facts which have been presented above are mainly of interest for two reasons. One is their possible usefulness in solving physical optic problems relating to underwater polarization in particular and to light penetration in general. The other is their potential helpfulness in evaluating the biological importance of submarine polarization patterns.

With relation to the first point, it is interesting that two of the main findings reported here were predicted on a theoretical basis before the present measurements were made (Waterman, 1954 a). These were (1) that polarized light would occur down to considerable depths in the sea, probably as far as the lower limits of the photic zone, and (2) that with increasing depth the influence of the sun's position on the pattern of polarization would gradually diminish in the upper few hundred metres after which it would be negligible. Both of these effects were clearly apparent in the present data; although at the maximum depth tested, 200 m, the sun's position still had considerable effect, it was only about a third of what it would have been near the surface.

Note that these predictions were made on the assumption that Rayleigh scattering of unpolarized directional light in the water was the basis of the primary underwater polarization pattern and on the currently accepted ideas about the directionality of deep-water illumination (Whitney, 1941; Poole, 1945; Jerlov, 1951). The fact that the deep polarization as it was actually found matched the predictions in these respects is in turn putative evidence for the validity of these elements in the original analysis.

One might go a step further here and point out that, when the submarine polarization pattern itself is understood more thoroughly, instrumentation and methods like those used in this work might be a convenient way to study the general problems of directionality and scattering of light under water. For instance, one might study the refractive effect of abrupt density changes where these are inaccessible for direct observation (LIMBAUGH and RECHNITZER, 1955).

As to their biological interest, the present results would seem to be significant because they greatly extend the known regions in which those animals whose eyes are sensitive to them might detect natural patterns of underwater polarization. This would now seem to be indicated for a good part, if not all, of the photic zone. Similarly, the possibility of some sort of a polarized light sun compass, comparable to that used in the sky by bees, and other animals, has been extended under water at least to 200 m, since changes in the sun's position result in corresponding modifications of the polarization pattern that far down.

Of the several fields in which further research on the subject of underwater polarization and its significance may be profitable, the most interesting one related to the present deep-sea work would be the possibility of making measurements at still greater depths. Since a 20 sec exposure at f/2·8 was required to photograph the interference pattern at 200 m, the present method was being pushed close to its reasonable limit. This is obvious from the fact that the light energy penetrating the water mass would probably be reduced to 0·1 its value at 200 m by an additional 40–50 m of water. Hence to go from 200 m to 300 m would require 100 × as much time for comparable negative densities!

On the other hand, since directionality of penetrating light is maintained to the lower limit of the photic zone, even though obliquity is decreased eventually to zero, somewhat deeper measurements should be possible if the polarization pattern were photographed in an upward direction. At least the light intensity would be greater to a degree dependent on the relation between scattering and absorption in the water mass concerned (PETTIT, 1936; ATKINS and POOLE, 1952). However, the percent polarization due to Rayleigh scattering would approach zero along the axis of the directional light beam so that the interference figure would become weak or disappear.

In any case it would be desirable to attempt such measurements and discover which of the various factors are actually critical under these circumstances. The presence of upwardly directed "telescopic" eyes in some bathypelagic fishes like *Opisthoproctus* and *Argyropelecus* is suggestive of the biological importance of vertical illumination in deep water.

REFERENCES

ATKINS, W. R. G. and POOLE, H. H. (1952), An experimental study of the scattering of light by natural waters. *Proc. Roy. Soc., London*, B, **140**, 321–338.

CLARKE, G. L. (1941), Observations on transparency in the southwestern section of the North Atlantic Ocean. *J. Mar. Res.*, **4**, 221–230.

JERLOV, N. G. (1951), Optical studies of ocean waters. *Rept. Swedish Deep-Sea Exped.*, 1947–1948, **3** (1), 1–59.

LIMBAUGH, C. and RECHNITZER, A. B. (1955), Visual detection of temperature-density discontinuities in water by diving. *Science*, **121**, 395–396.

PETTIT, E. (1936), On the color of Crater Lake water. *Proc. Nat. Acad. Sci.*, **22**, 139–146.

POOLE, H. H. (1945), The angular distribution of submarine daylight in deep water. *Sci. Proc., Roy. Dublin Soc.*, 24, 29–42.

WATERMAN, T. H. (1950), A light polarization analyzer in the compound eye of Limulus. *Science*, **111**, 252–254.

WATERMAN, T. H. (1954 A), Polarization patterns in submarine illumination. *Science*, **120**, 927–932.

WATERMAN, T. H. (1954 B), Polarized light and the angle of stimulus incidence in the compound eye of Limulus. *Proc. Nat. Acad. Sci.*, **40**, 258–262.

WHITNEY, L. V. (1941), The angular distribution of characteristic diffuse light in natural waters. *J. Mar. Res.*, **4**, 122–131.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 435-437

Elevation of sea level caused by wind in a rectangular channel

By WALTER HANSEN

Summary—Inquiries are made into the rise of water level due to wind in a rectangular basin, and comparisons of the results made with observations during the storm surge on the Dutch coast in 1953.

IN ADDITION to normal tides, storm surges occur occasionally on the coasts of the North Sea, causing severe damage. In 1953, a storm surge—called the Holland Hurricane—caused especially serious devastation, not only in the Netherlands but also in Great Britain.

Both scientists and engineers are anxious to learn about the development of such storm surges as effected by the morphology of the sea bottom and the configuration of the coast bounding the respective sea area within the storm field.

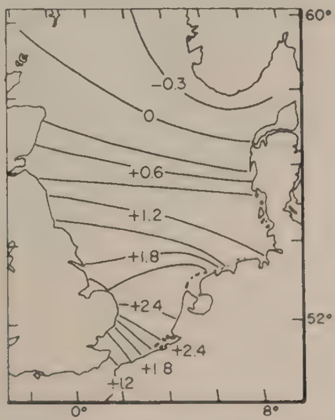

Fig. 1. Maximal elevation of the storm surge of 31 January in the North Sea. (From ROSSITER.)

The following account deals with an experiment to detect the changes of sea level for a given wind field. Only a large-scale survey can be described here; detailed investigations are planned and —thanks to the kindness of Professor ROSSBY—will be carried out on the BESK in Stockholm.

Details of the problem are as follows:

The elevation of water-level produced in a local, constant wind field, but variable with time, can be numerically ascertained in a rectangular basin corresponding in its position and dimensions approximately to those of the North Sea.

The quantitative relation between known and unknown magnitudes is given by hydrodynamical differential equations. As the configuration of the bottom, the Coriolis force and friction will be considered, it is not possible to represent the solution in final analytical form. This is true also if—as is assumed here—there is no mass transport perpendicular to the coast. Likewise the transport of water masses across the northern limit of the basin has been assumed to be zero. The problem therefore has to be treated numerically. For this purpose a system of differences equations was derived from hydrodynamical differential equations. These make it possible to determine the elevation of sea level due to wind and the components of the transport of the water masses at the points of intersection of a grid spread over the North Sea. Details of this method are given elsewhere (HANSEN, 1954).

The grid used has been inserted on Fig. 1. The wind field, used as a basis, has the same wind direction throughout, parallel to the longer side of the basin. It is assumed that the velocity of the wind is described as a sine function of the time co-ordinate having for all points on the grid the same amplitude and phase. In the numerical calculation, carried out for the values of 0 to π, related to a time interval of 12 hours, the amplitude of the wind velocity has been chosen as 20 m/sec.

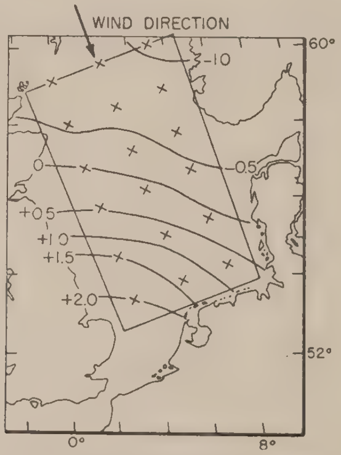

Fig. 2. Maximal elevation of a storm surge in the North Sea based on theory for a rectangular basin of variable depth

For the tangential stress which the wind exerts on the surface of the sea, the value in SVERDRUP, JOHNSON and FLEMING (1942) of $3{\cdot}2 \times 10^{-2} \times W^2$ was used, where $W(m/sec)$ stands for the velocity of the wind.

The friction in the water is directly proportional to the current velocity or to the gradient of the surface of the sea.

The accessory value of the friction depends not only on the depth of the water but also on the maximum velocity. For a water depth of 50 m and a velocity of 1 m/sec this has a value of $0{\cdot}48 \times 10^{-4}$.

The numerical solution is found by applying the method of differences which has been described in the paper mentioned above.

In Fig. 2, the calculated lines of equal maximum elevation has been inserted. While in the northern part of the basin a trifling fall of water level can be observed, the elevation increases generally towards the south. The higher values in the western parts of the basin are noteworthy, being apparently a result of the Coriolis force as well as of the depth distribution. In the regions to the east the values are considerably smaller. As the calculation is only a rough one, details of the distribution of elevation are not considered.

Fig. 1 comprises the lines of equal maximum elevation values for the Holland Hurricane from a paper by ROSSITER (1954). GROEN (1953) in his investigations in general obtained similar results. Both papers are based essentially on the observed elevations of the sea level along the coasts.

The trend of the calculated curve in Fig. 2 coincides in its characteristic features with those given by ROSSITER and GROEN. The calculated maximum elevation is about 2·0 m, the observed values in this area during the Holland Hurricane being 2·4 m.

REFERENCES

GROEN, P. (1953), Voorlopig onderzoek van de waterstanden opgetreden langs de kusten der Noordzee op 31 Jan. en 1 Feb. 1953. *Kon. Nederl. Meteorolog. Inst., Afd. Oceanogr. en Marit. Meteorol., Rapp.*, **4** (6), 1–5.

HANSEN, WALTER (1954), Über ein Verfahren zur Ermittlung der Gestalt der Meeresoberfläche bei zeitveränderlichem Windfeld. *Deutsche Hydrogr. Z.*, **7** (1/2), 15–22.

ROSSITER, J. R. (1954), The North Sea storm surge of 31 January and 1 February 1953. *Phil. Trans. A*, **246** (915), 371–400.

SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. H. (1942), *The Oceans: their physics, chemistry and general biology*. Prentice-Hall, Inc., New York, 1087 pp.

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On the breeding areas of the Swordfish (*Xiphias*)*

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Summary—The Danish oceanographic expeditions with the Research Steamer *Dana* and other ships have obtained about 60 postlarval stages of *Xiphias* (between 5 and 46 mm in length) from all oceans. Most of these, however, were taken in the western North Atlantic.

The distribution of the smallest stages (i.e. smaller than 20 mm in length) indicates that an important breeding area lies north and northeast of the Lesser Antilles in the southern part of the Sargasso Sea. Breeding areas are also indicated by records of small postlarvae west of Sumatra, in the South China Sea, in the Celebes and Banda Seas and off the Marquesas.

Some spawning occurs during all seasons, but maximal spawning seems to take place during February–April in the North Atlantic. Spawning probably takes place at the same season in the western Pacific, but it occurs later in the year in the Mediterranean owing to the special temperature conditions there. The fry are usually found in water of about 24° C. or higher. They are generally captured between the surface and a depth of about 30 metres. The material at hand seems to show a growth rate of about 8 cms during the first year, but sufficient material is not yet available for an accurate determination of the growth rate. The fry preferably feed on fish larvae up to nearly the same size as the small voracious *Xiphias* larva itself (Fig. 1). Figures are given of three developmental stages and outline charts show where fry have been taken. Fishing for swordfish may be possible (by floating lines) in the main spawning area in the western North Atlantic.

RECENTLY THE importance of large oceanic fish has increased commercially as well as in sports fishing. It has therefore become not only desirable, but also possible, to broaden our knowledge of the fish fauna on the high seas. Among these large fish, the swordfish (*Xiphias*) is the most appreciated by epicures and sportsmen alike. Although landings of this fish have increased greatly in the last generation, our knowledge of this species still leaves much to be desired. Recently, however, ARATA (1954) has made a valuable contribution to its biology, including a description of its earliest development. Therefore, detailed description of the various developmental stages is omitted here, but we have included a few figures of them (Fig. 1).

While many pelagic fish are represented by enormous numbers of fry in the material collected by the *Dana* and other Danish vessels, this is not the case for several of the large species, e.g. the tunny and bill-fish. Thus far, only 500 specimens of the latter have been found in more than 3000 pelagic samples. Some 400 of these belong to the *Istiophoridae*, and only about 60 to the *Xiphiidae*.

The reasons that so few specimens are taken in the youngest stages (about 5–45 mm in length) is undoubtedly chiefly due to the fact that the fry of these large predators of the sea are relatively scarce in comparison with the abundance of the fry of smaller species, and to the fact that they very quickly attain a size which enables them to escape the gear (2 or 1½ metre ring net of stramin or coarse silk) generally used by the *Dana* in catching fish fry. By the time *Xiphias* fry reach a length of about 12–13 mm, they attain sufficient swimming speed to escape the nets (generally towed at a speed of about 1 metre per second). Thus, only about 20% of the fry caught are over

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* Papers from the *Dana* Oceanographical Collections No. 45.

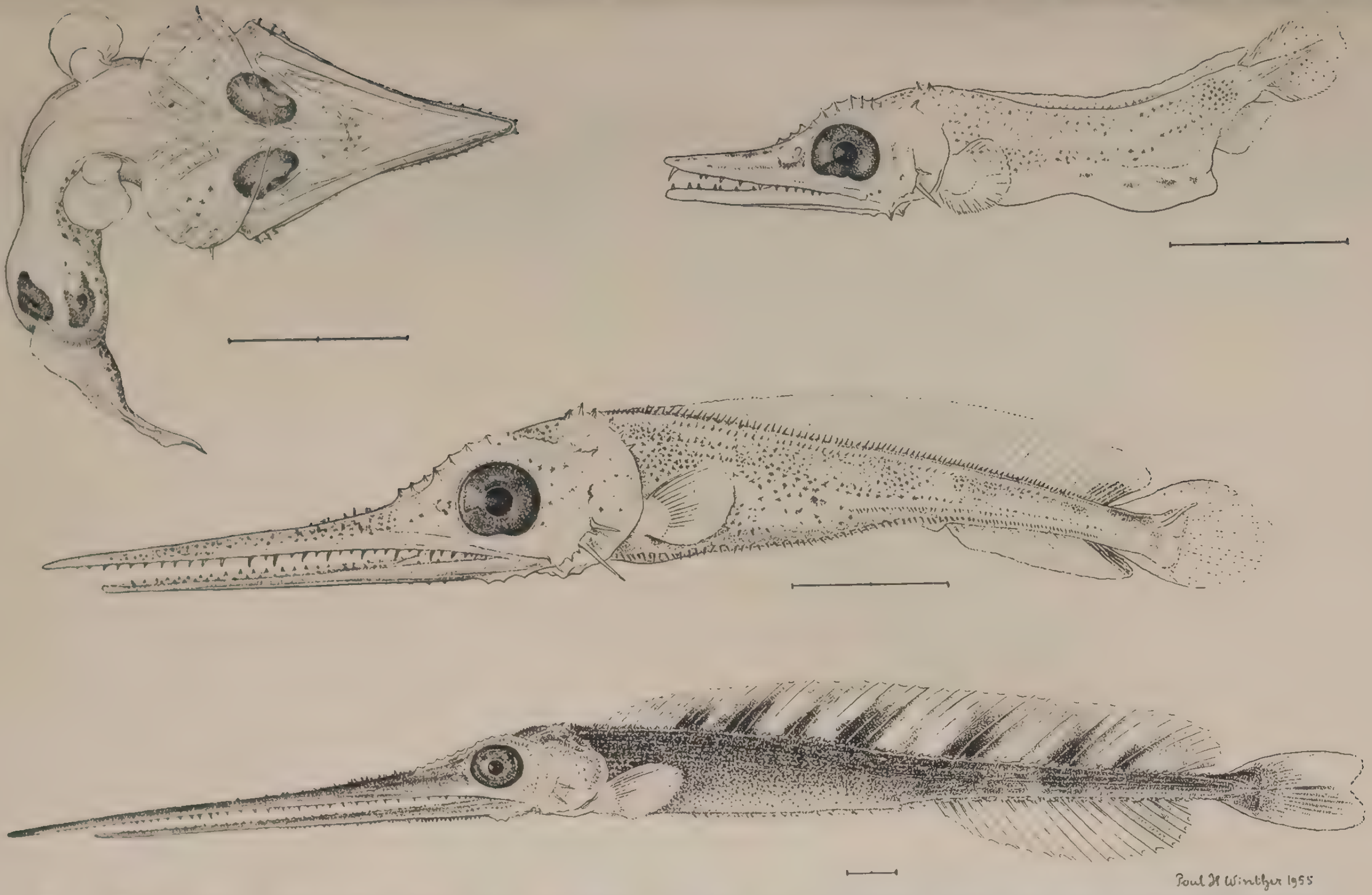

Fig. 1. *Xiphias gladius*. Postlarval stages from the North Atlantic. Top, left: 8·2 mm, seen from ventral side; the specimen has swallowed another fish larva (*Dana*, St. 1280). Top, right: 7·9 mm (*Dana*, St. 1280). Centre: 15·6 mm (*Dana*, St. 1293). Bottom: 46·3 mm (*Dana*, St. 3542). Rule: 2 mm.

13 mm in length, and none are over 46 mm. A further reason for the infrequent catches of the fry is that they live near the surface. On the *Dana* expeditions, a ½-metre ring net was usually used in the surface layers rather than a larger one. Even small fry can certainly avoid such a small net. That the fry do indeed frequent the surface layers is also indicated by the fact that the specimens discussed by CHR. LÜTKEN (1880) were collected from a sailing ship at the surface. In addition, most of the 34 *Xiphias* specimens described by ARATA (1954) were small (chiefly 2–3 cm in length), and were taken at the surface in a dipnet during the day. Therefore, in the future some attention should certainly be given to using this or some similar sampling method to delimit the areas frequented by *Xiphias* fry.

As we shall see later, catches of the young stages of *Xiphias* in the *Dana* collection presumably were chiefly taken while the nets were being hauled in, especially when these nets, which had no closing device, were fishing the surface layers just before being hauled in over the ship's side. Furthermore the adult swordfish is a solitary creature and never moves in schools. The scattered catches of the young stages suggests that this habit may be established very early in development.

So few *Xiphias* fry have been reported that they provide only a very limited amount of data for determining the more important spawning areas, the seasonal occurrence, and the vertical and horizontal distribution. Similarly, it is difficult to deduce the relationship between the distribution of the fry and environmental factors. Nevertheless, the material at hand does yield more information than has previously been obtained from earlier, more scattered observations. Therefore, I shall outline the chief points that appear to be indicated by the evidence at hand with the hope that eventually sufficient data will be accumulated to outline the complete life history of this interesting fish.

The map (Fig. 2) with the locations from which Danish vessels have taken specimens of *Xiphias* fry shows that the material comes almost exclusively from the area around the West Indies and the southern part of the Sargasso Sea, and from Indo-Malaya. The former area has yielded by far the greater proportion of these since the Sargasso Sea area has been fished especially intensively and at various times of year. The present paper chiefly aims, therefore, to add to our knowledge of the breeding areas of *Xiphias* in the western part of the North Atlantic.

HORIZONTAL DISTRIBUTION OF FRY

Most of the *Xiphias* specimens from the western part of the North Atlantic were taken on the expeditions of the Motor Schooner *Dana* in April–July 1920, and in February–May 1921, furthermore, on the expeditions of the Research Steamer *Dana* in November–April 1921–1922, and in August 1928. These voyages were undertaken in connection with the investigations of JOHS. SCHMIDT on the breeding areas of the fresh water eel and most of the stations were therefore taken in the Sargasso Sea and adjacent areas.*

We will first consider the distribution of catches of *Xiphias* fry from this area, and the temperature conditions at the localities where they occurred. The captures of

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* See list of references for the reports of these expeditions. From these it can be seen how extensive is the network of *Dana* stations in the Atlantic.

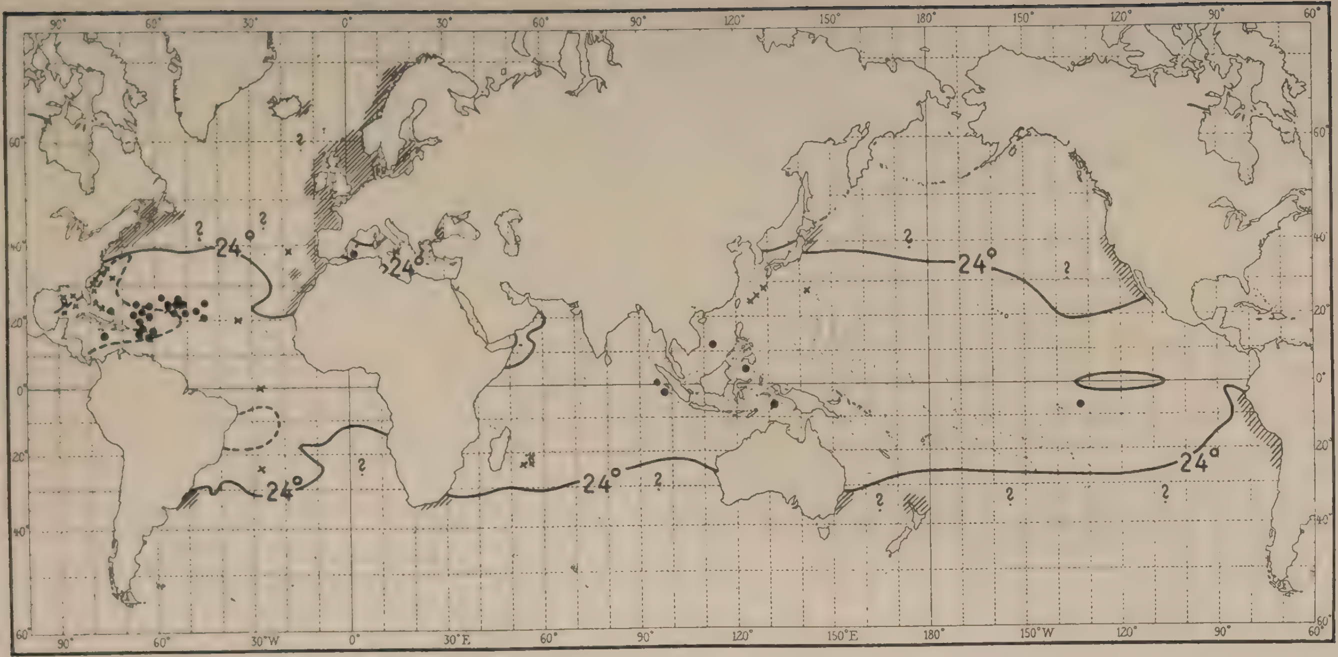
90°
60°
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Fig. 2. Records of *Xiphias* postlarvae smaller than 100 mm. ● *Dana* records, × other records. Summer surface isotherm for 24° C is indicated (from Sverdrup, Johnson and Fleming 1942). (Northern hemisphere: August; southern hemisphere: February). – – – – 23° C isotherm in 100 metres depth in the Atlantic (from Schott 1912). //// Dispersion of adult *Xiphias* north and south of the 24° surface isotherm during the northern and southern summer respectively; records from continental waters only available.

Xiphias in the Sargasso Sea were not in general from the central part of this area where the most concentrated fishing has been carried out and where the young *Anguilla* larvae have mostly been taken. On the contrary, the specimens were chiefly taken in the southern part of the Sargasso Sea, down toward and among the West Indian islands and thence northeastward. This distribution is clearly illustrated along the track of the Motor Schooner *Dana* in 1921 (Fig. 3). The ship left St. Thomas late in February and surveyed the area between about 20° N and 30° N and 45° W to about 67° W until mid-May. No *Xiphias* fry were taken north of 23° 10′ N, but catches were made at almost all of the southern stations. These extended over the entire section fished between about 45° W and 67° W. At those stations, where the majority of the catches were made, the surface temperatures were about 25° C or more. At two stations, it was 24° C and at only one was it as low as 23·5° C. This locality was not far from an area where the temperatures were 24° C. Fig. 3 shows the positions of the catches in relation to the surface isotherms for 24° C and 25° C. The preceding year (1920), when the Motor Schooner *Dana* left the Mediterranean for this area in late April, *Xiphias* fry were taken as soon as the ship entered water where the surface temperatures were more than 24° C. Then, due to a leak, the schooner was forced to go directly to St. Thomas without making further observations, and could not return to the area before June. At that time, the surface temperatures were 25° C or higher over almost the entire area under consideration, north to about 35° N Lat. (Fig. 4). Despite numerous stations mainly north of 27° N Lat., only a very few *Xiphias* fry were taken in that area, the northernmost being at 26° 19′ N Lat. Therefore, the swordfish's principal spawning season in this area seems to be over by early summer (June).

During the winter of 1921–1922, the Research Steamer *Dana* was in this part of the Atlantic with headquarters at St. Thomas and St. Croix. The ship left the Cape Verde Islands on 3 November heading for French Guiana. It arrived at Barbados on 22 November and proceeded among the Lesser Antilles to a locality east of Barbuda before the first *Xiphias* fry were caught. Since the surface temperatures throughout the area across the Atlantic to Barbuda were between 25° C and 29° C, temperature is not the only factor which limits the distribution of the fry. In December, the vessel worked in the vicinity of St. Croix and then in January on her return from the Pacific (through the Panama Canal), she continued around Cuba to Florida, Haiti and back to St. Croix for further work in that area during March and April. Fishing with pelagic nets was particularly carried out at a locality just west of St. Croix, and here 20 specimens of *Xiphias* fry, chiefly early stages of 5–10 mm, were caught. Some few specimens were caught in other parts of the West Indies area. It may be that the connection with the open Atlantic through the Anegada Passage has something to do with the frequent presence of fry in this particular area. Later in April, the vessel continued into the central portion of the Sargasso Sea, but no *Xiphias* fry were taken there.

In 1928, on the world cruise, the *Dana* went from the Mediterraenean across the Atlantic towards Panama. In the middle of August, the ship passed through the area where most of the *Xiphias* fry had previously been caught. There the *Dana* again caught *Xiphias* fry at every station. Of eight specimens captured, half were 17–46 mm in length and half 6–10 mm. The surface temperatures at this time ranged from 27°–28° C. No more specimens were taken, however, after entering the Caribbean.

In 1911, and for many years thereafter, JOHS. SCHMIDT arranged with various Danish merchant vessels as well as with the Schooner *Margrethe* to fish for eel larvae with pelagic nets, especially in the surface layers of the Atlantic. Later, from 1929 to 1938, the collecting was extended to the Pacific. A few *Xiphias* fry were found in these samples. These individuals were all taken in the area outlined above, i.e. in the especially warm parts of the western Atlantic where there are high temperatures down to a depth of at least 100 metres. When all the Danish records together with the localities for *Xiphias* fry given by ARATA (1954) and by LÜTKEN (1880) in the Atlantic Ocean are plotted (Fig. 2), it is obvious that the portion of the western Atlantic just described, and parts of the Caribbean, must be considered as the most important spawning area for this species in the North Atlantic. Thus, all of ARATA's and some of LÜTKEN's specimens came from the western Atlantic and Caribbean. LÜTKEN's specimens in the Zoological Museum, Copenhagen, range from 10 to 51 mm in length, but only one is smaller than 20 mm in length.

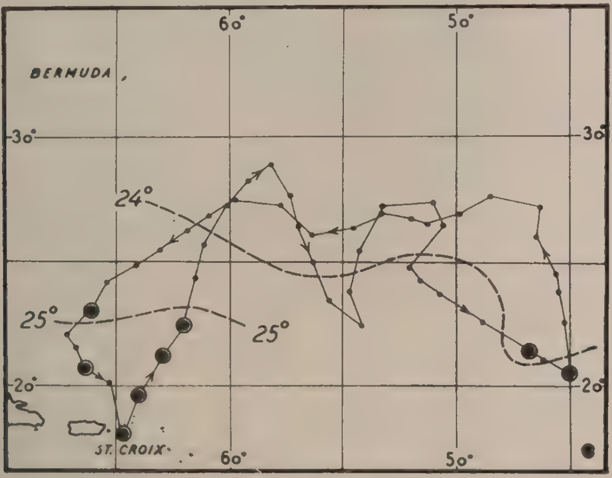

Fig. 3. Records of *Xiphias* postlarvae obtained during the cruise, February–May 1921. ● positive stations, · negative stations. Surface isotherms for 24° C and 25° C indicated.

Despite the extensive collecting by the *Dana* in the Indo-Pacific, especially in the Marquesas–Fiji area, north of New Guinea, Malaya, west of Sumatra and in the Madagascar area, only very few specimens were found (a total of seven specimens, 4·9–17·1 mm in length). These were limited to the area west of Sumatra, the South China, Celebes and Banda Seas and off the Marquesas. LÜTKEN (1880) also mentions a few catches from a merchant ship (commanded by Captain A. F. ANDRÉA) from the Reunion area (Fig. 2), the lengths of three of these specimens (preserved in the Zoological Museum, Copenhagen) are 29·0, 29·5 and 44·5 mm. In addition to these, fry are known in the Pacific, from the North Equatorial Current and from the Kuroshio Current (YABE, 1951; NAKAMURA, 1951). We know of no other records of fry from the Atlantic or Pacific Oceans. Therefore, the boundaries of the breeding areas in these waters cannot be more sharply defined until more specimens are obtained.

SEASONAL DISTRIBUTION OF FRY

Southwestern North Atlantic. To find the breeding areas of a species, the smallest larval stages are the most important, because these are carried by currents alone for comparatively short distances from the spawning area itself. Therefore we will consider only those specimens in postlarval stages smaller than 20 mm in length, in examining the seasonal distribution. As shown below, it is unlikely that any of the postlarval stages were taken in depths greater than 200 metres. Certainly they belong to the warmest, upper water layers, so that we need only consider the nets which fished with 600 metres of wire out or less, because these nets undoubtedly fished only in the upper 200 metres of the sea.

Since various sizes of nets were used, the fishing time was calculated as the number of hours a stramin ring-net 2-metres in diameter was towed.* In the areas where all the catches were made in the western North Atlantic Ocean, namely in the Caribbean Sea and that part of the Sargasso Sea between 15° N and 30° N and west of 40° W, there have been about 1690 2-metre-stramin-net hours fishing in the upper 200 metres of the sea.

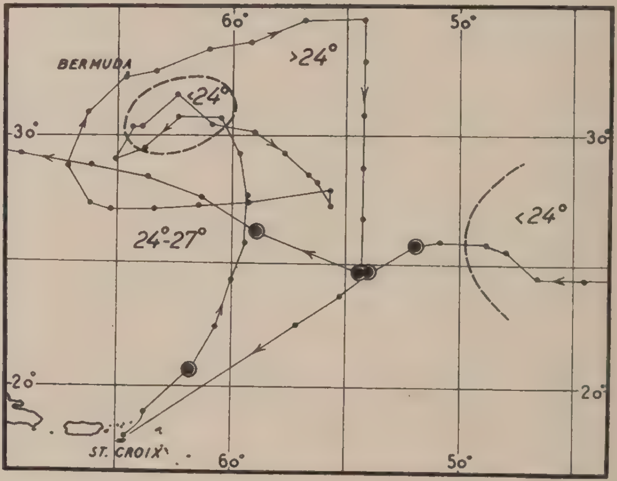

Fig. 4. Records of *Xiphias* postlarvae obtained during the cruise, April–July 1920. ● positive stations, · negative stations. Areas with surface temperatures below 24° C indicated.

From Table I, it can be seen that the postlarval stages smaller than 20 mm in length, which are mostly less than a month old, occur practically throughout the year. Even the smallest postlarval stages of 5–8 mm in length are found in nearly every month of the year. With so little material, no definite estimate of a peak season can be given. However, omitting the catches for July–September, when little fishing was undertaken in the area, and considering only those months when more than 100 hours or more of fishing actually took place, one notices that the biggest catches occurred in February–March–April. The preceding months show a consistent increase towards this maximum, while there is a decline in May through June. Thus, even if *Xiphias* breeds throughout the year in this tropical area, analysis of the data in this way suggests that the maximum is from February to April. ARATA (1954, pp. 234–239), on the other hand, from his own records and those of others which note the appearance of the fry or of mature specimens, concludes that the peak of the spawning season off Florida and Georgia is from April through September. In this connection, it should be noted that our data too indicate the presence of a large number in August (Table I). However, this figure is due to the fact that the *Dana*, on her passage through the southern part of the Sargasso Sea in 1928, chanced on six small specimens in postlarval stages and two a little larger (33·0 and 46·3 mm in length) at the three stations in that area. Consequently, it seems possible that this particular year was an unusually favourable one for the reproduction of this species.

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* One hour's fishing with this gear (S200) is calculated as equal to 2 hours with a 1½ m stramin net (S150) or silk net (P150), and to 4 hours with a 1 m stramin net (S100) or silk net (P100).

It should be stressed here that the area where the fry discussed in this paper were found *must* be one of the species' chief spawning areas, because equally intensive fishing in adjacent areas to the north and east was carried out from Danish vessels using the same type of gear without taking a single postlarval specimen. Although the area southeast of the main area was fished less intensively, it was sampled rather adequately without finding a single specimen. LÜTKEN (1880) mentions some catches (undated) of specimens in young stages, some as small as 2 cm in length, taken with drag nets at the surface from sailing ships in the centre of the tropical-subtropical Atlantic. Hence, we know that the species *must* also breed there as well. Undoubtedly, spawning is much more scattered there than in the area delimited by the Danish surveys. Thus, when the *Dana* crossed from Capetown to the Canary Islands via St. Helena–Freetown in February–March 1930, no *Xiphias* larvae were taken there despite intensive fishing. In any event, this does not seem to have been the right season to find them in this part of the eastern tropical-subtropical Atlantic.

Table I
The monthly distribution of catches and number of specimens in postlarval stages less than 20 mm in length per 100 hours of fishing

Month	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*	*X*	*XI*	*XII*	*Total*
No. hrs. fishing	45	156	274	365	164	214	44	20	4	113	61	216	1690
No. post-larvae <20 mm	1	6	12	14	0	1	2	6	0	1	1	5	49
No. per 100 hrs. fishing	2·3	4·6	4·4	4·0	0	0·5	4·5	30·0	0	0·9	1·5	2·3	3·0

Mediterranean. In the Mediterranean, where environmental conditions are suitable for the development of a rather sizeable stock of *Xiphias*, only a single *Xiphias* larva has been found to date in the Danish collections. It was taken in the Balearic Sea off Algiers in late September. At Messina (SELLA, 1911; SANZO, 1922; 1930), this species breeds in the summer (June–August) at a time when the surface temperatures become high enough (> 23°–24° C). Consequently, it is most peculiar that postlarval specimens were not taken during the *Thor* expedition in 1910, since considerable fishing was carried out with pelagic gear in July–August and in early September.

Indo-Pacific. The *Dana* in 1928–29 carried out approximately 1650 hours of pelagic fishing in the surface layers down to roughly 200 metres over wide areas of the Indo-Pacific (Fig. 2). Almost all of the tows were made in areas where the water temperatures were within the limits usual during spawning of this species. Nevertheless, only a few young specimens were taken there. These provide a very incomplete picture of the breeding areas and seasonal distribution. Except for a single specimen near the Marquesas Islands in late September, all of the others are from the Indo-Malaya region during the months of March, April, June, September and November or practically throughout the year.

As mentioned earlier, Lütken's specimens are undated so that they do not help to clarify this point. However, the postlarval specimens of 11–27 mm in length from the western Pacific mentioned by Yabe and Nakamura were taken from March to May. Consequently, the season seems to correspond to that of the western Atlantic.

VERTICAL DISTRIBUTION OF FRY

It has already been noted that all the evidence points to the fact that the fry are generally found in the uppermost water layers over deep water. The distribution also suggests some connection with island areas (i.e. West Indies, Indo-Malaya, East China Sea, Mediterranean). The reason may be that there is more food in such areas than in the open ocean. Since we only have any significant number of *Xiphias* fry from the western part of the North Atlantic, as previously pointed out, we will delimit the water layers where the fry were taken in that area and consider the size differences at various depths. The material included only two specimens over 2 cm in length: one 33 mm in length, which was taken in a net which was fished at a depth of approximately 30 metres, and one 46·3 mm in length which was taken in a dipnet at night with a light. Therefore our discussion of vertical distribution will include only a consideration of specimens of less than 2 cm in length.

The 53 specimens (< approximately 20 mm) caught in this area of the Atlantic were taken in 43 hauls of the pelagic net. The number per tow was 1 specimen in

Table II

Distribution of Xiphias *fry according to number and size of specimens and the depth of towing*

Metres of wire out	*Approximate depth of capture in metres*	*No. of specimens < 20 mm*	*No. of hrs* fishing*	*No. of specimens per 10 hrs fishing*	*Size range in mm*	*Average size in mm*
Surface–65	0–ca. 20	16	61	2·6	5·9–16·3	8·5
80–100	ca. 30	20	61	3·3	5·8–18·6	9·7
150–200	ca. 50–70	5	35	1·4	6·3–18·2	10·6
300–600	ca. 100–200	8	110	0·7	5·7–20·0	11·2
700–5000	>ca. 230	4	75	0·5	5·6–15·6	10·7

* See p. 444 and footnote on that page for method of calculating fishing hours. The number of fishing hours includes only those stations where specimens were taken.

35 hauls, 2 in 7 hauls,* and 5 in 1 haul, fished at approximately 30 metres. It was exceptional therefore for more than one specimen to be taken in a haul. This indicates that the fry are scattered, and that they often may be captured when the net is being drawn in. From Table II, it appears that the postlarval stages are to be found chiefly in the upper 30 metres. Furthermore, the smallest specimens of 5–6 mm in length were taken in nets which fished for one or more hours at depths down to more than 230 metres. Hence, it is likely that the great majority, perhaps all, of the smaller specimens taken in the nets which were towed rather deep below the surface were actually caught when the nets were being drawn in.

The specimens taken in nets towed in the upper 30 metres were on the average the smallest. This may mean, as it does for the postlarval stages of many other oceanic species, that larger specimens are found deeper than the smaller ones. The latter, we must assume, remain chiefly at the surface where the pelagic eggs presumably float. The small size of our nets and the fact that these were not closing nets makes it impossible, however, to reach any final conclusion on this point. LÜTKEN'S and ARATA'S findings show, however, that the fry do not avoid strong sunlight in the uppermost layers of the sea. They found postlarval stages of 10 mm and up to 5–8 cm at the surface both during the day and at night. Thus, LÜTKEN has, as already mentioned, records from the Atlantic and Indian Ocean (Fig. 2) taken with a drag-net at the surface. ARATA'S series of postlarval specimens and of the adolescent stages of 6·3–80·9 mm from the Gulf of Mexico and Straits of Florida were for the most part taken at the surface in dip-nets. For the time being, it is not possible to determine whether most of the postlarval stages live just below the surface or whether they live somewhat deeper, perhaps within the upper 30 metres.

The few Danish specimens of *Xiphias* from the Indo-Pacific show a vertical distribution similar to that in the Atlantic. Two specimens were taken with 50 metres of wire out, one with 100 metres of wire out, three with 200 metres of wire out and one with 350 metres of wire out. This means that they were from depths of 15–100 metres, unless they were captured when the gear was being hauled in. The size of the specimens ranged from 4·9 to 17·1 mm in length.

ENVIRONMENTAL FACTORS AND THE DISTRIBUTION OF THE FRY

Temperature. The influence of temperature on the distribution of the fry was described above. It is clear that, in the breeding season, *Xiphias* seeks tropical or subtropical areas with high surface temperatures. Although the species migrates far north or south in northern or southern summers respectively, to feed where the water masses have temperatures as low as 12°–13° C or a little lower,† during the breeding season it must migrate to areas where the temperatures are not lower than 23·5° C, more especially in water with temperatures between 25° and about 29° C, as shown by the fact that most fry have been taken at localities where the temperatures were within these limits. Presumably *Xiphias* remains close to the surface during spawning, but there is no definite information on this point. Since the temperature at depths of 75–125 m is less than 23° C at all localities where small post-larval stages have been taken, we may assume that the spawning fish do not go any deeper.

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* In one of these hauls from roughly 30 metres depth, one specimen was taken together with the 33 mm-specimen mentioned above. The latter is not included in the table.

† Since *Xiphias* remains in the Mediterranean throughout the year, it must be able to survive in water of 13° C, for the whole water mass falls as low as this in winter.

In the *southwestern North Atlantic Ocean* surface temperatures between about 23·5° C and 28·1° C have been encountered at all localities where postlarval stages have been taken. Surface temperatures of 24·5°–25·5° C are found during the breeding season from February–April, and this temperature seems accordingly to be the actual lowest spawning temperature. With the approach of summer the temperature rises to 27° to 28° C or a little higher, and then about October it begins to fall again to about 25° C.

In the *Mediterranean Sea*, the surface temperature where the one postlarva was taken was 23·8° C (late September). As already mentioned, spawning apparently takes place in the Mediterranean much later in the year than in the West Indies. The reason for this is apparently that the temperatures favourable for spawning are not high enough until somewhat later (in August it is about 23·3° C–26·5° C).

In *Indo-Malaya*, the surface temperature at the places where postlarval specimens were taken was generally higher than in the Atlantic (namely about 28°–29° C). In the *Pacific* at the Marquesas it was however only about 26° C.

Salinity. Young fry are known to exist at localities where the surface salinities range between about 33·8$^{\circ}/_{\circ\circ}$ and 37·4$^{\circ}/_{\circ\circ}$; but the adult fish is found at very different salinities, e.g. at 39$^{\circ}/_{\circ\circ}$ in the Mediterranean and at 6$^{\circ}/_{\circ\circ}$ in the Baltic. The species thus tolerates a wide range of salinities, but it is not possible with the material at hand to determine any correlation between salinity and the breeding habits of *Xiphias*, other than that the salinity must apparently be higher than 34·00$^{\circ}/_{\circ\circ}$. Thus, in the general area of the Caribbean, most of the fry have been taken in water with salinities of about 35·9$^{\circ}/_{\circ\circ}$–36·7$^{\circ}/_{\circ\circ}$ and in Indo-Malaya of about 33·9$^{\circ}/_{\circ\circ}$–35·5$^{\circ}/_{\circ\circ}$.

Light. Since fry up to 4–5 cm in length have been taken at the surface of tropical seas on clear, sunlit days, and have also been taken there at night with artificial light, this species lives close to the surface under varying light conditions in a manner contrary to many other oceanic species. It is not definitely known how deep they can live and thrive.

GROWTH AND FOOD

Very little is known about the growth of the swordfish. So far as I am aware, no one has made age analyses from the bones or otoliths even in areas such as the Mediterranean where small specimens are regularly caught. SANZO (1922) has reported on the growth under laboratory conditions of newly hatched larvae for a period of ten days.

A review of the postlarval specimens from West Indian waters (ARATA'S and the Danish material combined), although based on fewer than 100 specimens, gives some indication of the growth rate (Table III). Although the method of collection was not the same and the intensity of fishing varied from month to month, it appears that spawning as already mentioned is particularly intense during the early spring. Table III seems to give a rather clear indication of the growth from the early stages (about 8 mm) in March–April to rather larger fry (approximately 23 mm) in July, and to fry of about 70 mm in length by the next spring. To what extent the latter represent the smallest of a larger and far more numerous 1-year group cannot be determined without more material. If specimens of 5–8 cm are representative of the 1-year olds, a specimen taken in May of 192 mm (ARATA, 1954) should be about 2 years old. This appears however to be far too slow a growth rate for a voracious species such as the swordfish. Unfortunately, NAKAMURA (1951) did not record the measurements of a rather large number of individuals of roughly this size found in the stomach contents of spearfish, measurements which would have provided some useful supplementary data on the growth rate of *Xiphias*. No further information is available on the growth although it is probably very fast, for such a predator, which, in the Pacific, may weigh up to 680 kgs.

Table III

The size of swordfish fry in different months based on the data of ARATA (1954) *and the Danish material*

Size	Month																	
mm	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI
80–84	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
75–79	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.
70–74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
65–69	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
60–64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
55 59	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
50–54	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
45–49	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
40–44	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
35–39	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.
30–34	.	.	.	.	1	.	3	1	.	.	.	.	.	.	.	.	.	.
25–29	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.
20–24	1	.	1	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.
15–19	.	2	.	1	.	.	1	3	.	.	.	1	.	.	.	.	.	.
10–14	.	2	2	3	.	.	2	1	.	1	1	2	.	.	.	.	.	.
5–9	1	2	9	13	1	3	2	2	.	.	1	2	.	.	.	.	.	.

The stomach contents of young stages indicate that the fry in the postlarval stages very soon progress from a copepod to a pure fish diet. Indeed, they often prey on close relatives (ARATA, 1954). To show how greedy this species is even in very early stages, we need only refer to Fig. 1. It shows a postlarval specimen of about 8 mm which has swallowed another fish larva, almost as large, so that the specimen appears to have eyes at both ends. The prey was swallowed head first. This was also the case in three other *Xiphias* specimens from the same haul with the prey in various stages of digestion. This exceptional catch of 5 postlarval specimens of 7–9 mm in one net, four of which were stuffed with food, suggests that they had become sluggish as a consequence. Thus, this may explain why so many were taken at one time. Normally, the majority would have escaped the net. Thus, it appears that even such small individuals must be very swift swimmers.

From our study, it is apparent how little is known of the breeding places, although it is clear that spawning takes place over all oceans where the surface temperatures are more than 23°–24° C. Little is known of the fry's migration away from the principal breeding areas and of the mature fish's migrations except in certain coastal areas. For example, it is not known whence come the migrants to northwest European waters during the summer and fall months, whether from the stock in the vicinity of the Iberian peninsula and the Mediterranean or from that of the western Atlantic.

With the development of fisheries for large pelagic, predatory species out on the open ocean, it is conceivable that a fishery can be developed in the chief Atlantic spawning area (floating line fishery).

In this and other areas of the open ocean there are also spawning places of other large pelagic fish. The closely related family of the Istiophorids is found in rather large numbers—we have over 400 postlarval specimens from all seas—in the same areas as *Xiphias* as well as over a large part of the Sargasso Sea. In contrast to *Xiphias*, we have however found numerous Istiophorids in the Madagascar area and many west of Sumatra. Otherwise there were relatively few Istiophorids in Indo-Malaya. As for *Xiphias*, the Istiophorids fry were totally absent in an area just north of New Guinea which has been intensively surveyed. The hydrographic conditions there gives no clue as to the reason for this. In the Samoa-Fiji area, there were a number of Istiophorid fry, but none of *Xiphias*.

From the above it becomes clear that, despite the extensive surveys of the Danish Oceanographic Investigations, relatively little has been learned of the life history of these large oceanic fish. Real progress on these problems can only be made with greater co-operation among the research organizations of the world. Thus, much useful information might be obtained with only a few extra hours of work in areas from which we have no records. It should moreover be noted that other fast predatory fish (*Coryphaena*, *Istiophorus*, etc.) are better able to catch fry which swim as swiftly as the *Xiphias* fry than is man. Collection of stomach contents of large predatory fish should accordingly always be carried out when possible.

REFERENCES

Arata, G. F., Jr. (1954), A contribution to the life history of the swordfish, *Xiphias gladius* Linnaeus, from the south coast of the United States and the Gulf of Mexico. *Bull. Mar. Sci., Gulf and Caribbean*, **4** (3), 183–243.

Bigelow, H. B. and Schroeder, W. C. (1953), Fishes of the Gulf of Maine. *Fish. Bull., U.S. Fish and Wildlife Service*, (*Fish. Bull.* 74), **53**, 1–577.

Carlsberg Foundation (1934), Introduction to the reports from the Carlsberg Foundation's Oceanographical Expedition Round the World, 1928-30. *Dana-Rept.* **1**, 1–78.

Goode, G. B. (1883), Materials for a history of the swordfish. *Rept. U.S. Comm. Fish and Fish.* for 1880, 289–394.

La Monte, F. (1944), Note on breeding grounds of blue marlin and swordfish off Cuba. *Copeia*, 1944, (4), 258.

Lütken, Chr. (1880), Spolia Atlantica. Bidrag til Kundskab om Formforandringer hos Fiske under deres Vœxt og Udvikling, sœrligt hos nogle af Atlanterhavets Højsøfiske. *Vidensk. Selsk. Skr.* (5), **12**, 441–447.

Nakamura, H. (1951), Notes on the life history of the swordfish, *Xiphias gladius* Linnaeus. *Japanese J. Ichthyol.* **1** (4), 264–271.

Sanzo, L. (1922), Uova e larve di *Xiphias gladius* L. *Mem. R. Com. Talassograf. Ital.*, **79**, 1–17.

Sanzo, L. (1930), Giovanissimo stadio larvale di *Xiphias gladius* L. di mm. 6, 4. *Mem. R. Com. Talassograf. Ital.*, **170**, 1–8.

Schmidt, Johs. (1912), Introduction. *Rept. Danish Ocean. Exped.*, 1908–1910, *to the Mediterranean and adj. Seas*, **1**, 1–49.

Schmidt, Johs. (1919), Stations in the Atlantic, etc., 1911–15, with two charts and introductory remarks. *Medd. Komm. Havundersøgelser*, (*Fisk.*), **5** (7), 1–27.

Schmidt, Johs. (1929), Introduction to the oceanographical reports including list of the stations and hydrographical observations. *Danish "Dana"-Exped.*, 1920–22, *in the N. Atlantic and Gulf of Panama, Ocean. Repts.* No. 1, 1–87.

Schott, G. (1912), Geographie des Atlantischen Ozeans. Hamburg, 330 pp.

Sella, M. (1911), Contributo alla conoscenza della riproduzione e dello sviluppo del Pesca-Spada (*Xiphias gladius* L.). *Mem. R. Com. Talassograf. Ital.*, **2**, 1–16.

Sverdrup, H. U., Johnson, M. W. and Fleming, R. H. (1942), The Oceans: their physics, chemistry and general biology. Prentice-Hall, Inc., New York, 1087 pp.

Tåning, Å. V. (1944), List of supplementary pelagic stations in the Pacific Ocean and the Atlantic, with an introduction. *Dana-Rept.* **26**, 1–15.

Yabe, H. (1951), Larva of the swordfish, *Xiphias gladius*. *Japanese J. Ichthyol.*, **1** (4), 260–263.

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Factors affecting productivity in fertilized salt water*

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Summary—The response of phytoplankton populations to added nutrients was studied by filling large out-of-door concrete tanks with sea water, and adding phosphate and nitrate. In general there was an immediate increase in photosynthesis and in growth of the population. In some cases, but not all, addition of phosphate alone was ineffective.

A large part of the variation in photosynthetic rate over a 40-day period is attributable to variation in the amount of light falling on the tanks, in the chlorophyll content of the phytoplankton, and in the phosphate concentration in the water. Large variations in the qualitative composition of the population had no apparent effect on this relation. The efficiency of the population in using light varied directly with the amount of fertilizer added, but not in proportion to it. Addition of nutrients to the bottles in which measurements of photosynthesis were made permitted evaluation of limiting factors.

The rate of phosphorus absorption, measured either as decrease of phosphate in the water or increase of phosphorus in particulate form, was directly related to the rate of photosynthesis.

INTRODUCTION

THE STUDY of phytoplankton production in fresh and salt waters has been hampered by a paucity of experimental techniques applicable to large bodies of water; it is difficult enough to make the necessary observations. The invention of the suspended bottle method of measuring population growth and photosynthesis (WHIPPLE, 1896, GAARDER and GRAN, 1927) was a long step forward, but it is desirable that techniques be invented and improved to the extent that various population functions can be effectively studied beyond the limits set by observation alone. Knowledge of algal physiology is at present too limited to permit widespread ecological prediction of the detailed behaviour of populations. Enough is known of the complex relations existing in natural habitats to make it clear that there is a need for developing methods of assessment of the condition of natural populations as they occur, and of the operation of environmental factors. Since large bodies of water are difficult to experiment with, save in the crudest way by mass fertilization, the most promising approach seems to involve manipulation of samples of natural populations. For example, HUTCHINSON (1941) was able to demonstrate that both nitrate and phosphate were acting as limiting factors to photosynthesis in Linsley Pond on several occasions by enriching the bottles in which measurements of photosynthesis were being made. NELSON and EDMONDSON (in press) used similar methods with photosynthesis and population growth preliminary to fertilizing a lake. LUND (1949; 1950) was able to evaluate limiting and controlling conditions in lakes in detail by such manipulation.

Furthermore, while the physiological role of chlorophyll has been elaborately studied, more information is needed on the ecological role of chlorophyll. Various studies have shown that, in a variety of aquatic populations, the rate of photosynthesis was closely related to the chlorophyll content of the plankton population, if proper allowance was made for light intensity (MANNING and JUDAY, 1941; review by EDMONDSON, in press).

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* Contribution No. 781 from the Woods Hole Oceanographic Institution.

The present paper is a contribution to the study of these matters. It briefly reports some of the main results of an investigation of the effects of added nutrients upon marine phytoplankton populations growing in large, out-of-door concrete tanks. It is based on the results of three experiments, one in 1947, two in 1948, and reference will be made to them by chronological number. Although several aspects of population biology were studied, the present paper is limited to a discussion of the effects of added nutrients upon the rate of photosynthesis, and relations with certain factors known to affect this rate. Since the work was undertaken with particular reference to the effect of fertilization on productivity of small bodies of salt water, high concentrations of nutrients were added. Nevertheless, the general approach is applicable to all aquatic communities including the ocean. The work followed the preliminary experiments by EDMONDSON and EDMONDSON (1947).

This is one of a series of investigations carried out at the Woods Hole Oceanographic Institution, Massachusetts, under the general supervision of Dr. GEORGE L. CLARKE. The author expresses his indebtedness to Dr. CLARKE and to Dr. C. O'D. ISELIN, then Director of the Institution, for making available an institutional fellowship and for support for the work. Thanks are due to Miss ROSEMARY HEWLETT who made all the counts of phytoplankton. Help with the work was received from a number of other persons, particularly Miss JEAN KEEN, Dr. B. H. KETCHUM, Dr. D. M. PRATT, Dr. W. S. VON ARX, Mr. ALBURT ROSENBERG, and my wife, YVETTE H. EDMONDSON. Financial assistance for some of the computation was received from the State of Washington Research Fund in Biology and Medicine (Initiative 171). A grant from the Agnes Anderson Fund of the University of Washington is gratefully acknowledged.

It is a pleasure to dedicate this paper to Professor HENRY B. BIGELOW, founder and former director of the Woods Hole Oceanographic Institution.

PROCEDURE

The tanks and most of the procedure and methods have already been described (EDMONDSON and EDMONDSON, 1947; PRATT, 1950). In the present experiments, one large concrete tank was divided by wooden partitions into four sections, each containing five cubic metres of water. The tanks were shaded by a whitewashed glass roof in order to reduce the inhibitory effect of full sunlight.

The tanks were filled by pumping sea water through two layers of #10 bolting silk to strain out the larger animals. After varying periods, sodium nitrate or dibasic potassium phosphate or both were added as concentrated tap water solutions, while the tanks were vigorously stirred with an oar. Subsequently, almost daily determinations were made of phytoplankton population, phosphate, oxygen, chlorophyll, light income, rates of photosynthesis and phosphate assimilation. Before each sampling, usually made between 7 and 9 a.m., the tanks were stirred. The morning temperature of the tanks was found to vary little over the entire period of time, and most of the temperatures were between 20 and 22°.

Usually there was no attempt to dislodge material from the sides. It was realized that periphyton would grow, but felt that, to achieve interpretable results, most of the work should be limited to the organisms which naturally would be found free in the water, rather than a heterogeneous mixture of plankton and dislodged periphytic organisms. In Experiment 3, the sides of one of the tanks were scraped down daily prior to sampling. This procedure dislodged sessile organisms, and had a profound effect on the phosphorus metabolism of the tank, as described by PRATT (1950).

Since the details of the fertilization are important, the schedule of additions of nutrients is shown (Table I). It will be noticed that in some cases phosphate was added before nitrate, and various time intervals elapsed between additions. The only method used not adequately described in existing publications is that used for measuring light.

An integrating photometer was used. The instrument was designed by Dr. W. S. von Arx and built by Mr. Robert Walden. It consists essentially of a photo-tube mounted under a flat sheet of flashed opal glass and fed by a constant-voltage power supply. The output, which varies linearly with the incident light, is fed into a condenser. The condenser, upon reaching a pre-determined voltage, is discharged by a thyratron tube, actuating a relay which operates a counter. The photo-tube used is RCS #926, which has its maximum sensitivity at 425 mμ and is relatively insensitive to red. The condenser was chosen to have a capacity such that the discharge interval is slightly less than one second in the brightest sunlight encountered in Woods Hole during the summer.

The instrument was calibrated in 1947 by comparison with an Eppley pyrheliometer mounted on the roof of the Oceanographic Institution at Woods Hole, and early in the summer of 1948 by similar comparison at the Blue Hill Meteorological Observatory. I am indebted to Mr. I. F. Hand for making the latter comparison possible, and Messrs. von Arx, Andrew Bunker, and Kenneth McCasland for the former. Values are given as visible light on the basis that one half the value given by the Eppley pyrheliometer is visible (see Edmondson, in press, for further discussion).

Reference will be made in this paper to the rate of photosynthesis; what was actually measured is the rates of oxygen change in illuminated and covered bottles suspended in the tanks for two-day periods.

Table I

Schedule of fertilization in the three experiments. Quantities of nitrogen and phosphorus are given as microgram atoms per litre

Date	*Tank* 1	*Tank* 2	*Tank* 3	*Tank* 4
1947 *Experiment* 1				
July 1	Tanks filled			
July 2	0	5P	10P	160N
July 3	0	80N	160N	10P
August 11	0	1P, 16N	0	1P, 16N
August 18	5P	0	0	0
August 25	0	0	5P	0
1948 *Experiment* 2				
June 28	Tanks filled			
July 2	5P	5P	5P	5P
July 6	80N	80N	80N	80N
1948 *Experiment* 3				
August 6	5P	5P	5P, 80N	5P, 80N*
August 23	80N	80N	0	0

* Walls of tank 4 were scraped daily.

EFFECT OF FERTILIZATION ON PHOTOSYNTHESIS

Bottles were filled and set out for the measurement of photosynthesis just before and just after addition of fertilizer. The two sets of bottles were therefore exposed to almost identical conditions, the only difference being in the amount of nutrient. As already reported (1947) the addition of such nutrients to natural populations increases the rate of photosynthesis greatly, as determined in four-day runs. In the present work, large increases in oxygen production were observed, up to an increase by a factor of as much as 5 (Fig. 1). It is interesting that the difference in order of addition of nitrogen and phosphorus in Tanks 3 and 4 in Experiment 1 appears to have made a difference in the subsequent behaviour of the populations. Addition of the large amount of phosphate in Tank 3 was not followed by an increase, whereas in Tank 2, a smaller amount of phosphate had doubled the rate. In Tank 4, nitrogen was added first and the subsequent addition of phosphorus had a further effect. The refertilization of Tank 3 on August 25 was followed by an increase in photosynthesis.

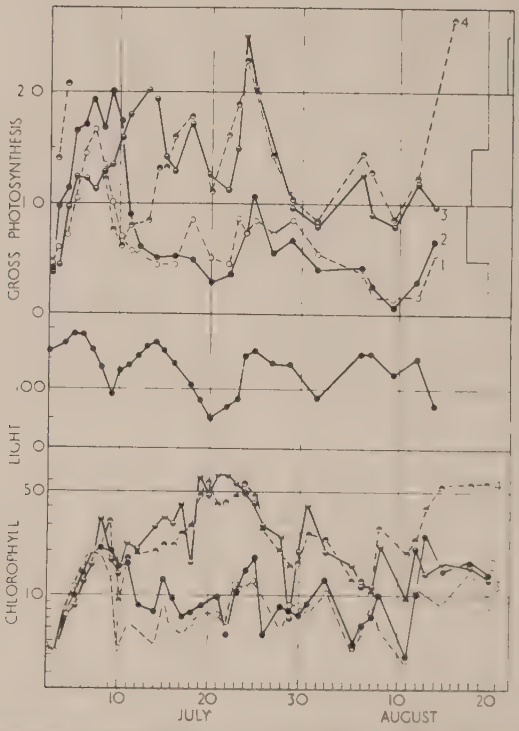

Fig. 1. Gross photosynthesis, incident light and chlorophyll in the four tanks. Photosynthesis as mg/l/day of oxygen produced, light as cal/cm^2/day of visible light, and chlorophyll as μg/l. Note that chlorophyll is plotted on a logarithmic scale. The first two sets of points in the top panel are for bottles filled on July 2 before and after the first fertilization. The histogram at the right of the top panel gives the relative frequency of the rates in the ranges shown.

It was necessary to know whether removal of the population from the open water to the tanks would have an effect aside from the effects of added nutrients. For that reason, in Experiment 2, fertilization with phosphorus was delayed for four days after filling, and addition of nitrogen delayed another four days. Population density and photosynthesis did not change significantly until after the second fertilization.

Fertilization was usually followed by an increase in population, but at first the increase was not as great as that in rate of photosynthesis, suggesting that lack of nutrients had been inhibiting the photosynthesis of the individual organisms.

After the initial increase in the rate of photosynthesis following fertilization, there were large changes in the rate in all four tanks. The changes will be discussed in detail only in Experiment 1. During this experiment, the values varied greatly, from a low of 0·07 mg/l/day of oxygen to a high of 2·50, mean 1·07, standard deviation 0·55 (Fig. 1). The mean values for the tanks separately for the period ending just before the fertilization of August 11 were 0·74, 0·90, 1·30 and 1·29 in order. The difference between Tank 2 and Tank 3 is significant to the 5% level of probability, but that between Tank 1 and Tank 2 is not quite significant. Tank 1 had been intended as a control, but failure of the caulking between Tanks 1 and 2 permitted some exchange of water. The increase of phosphorus in Tank 1 was 0·69 μg at/l.

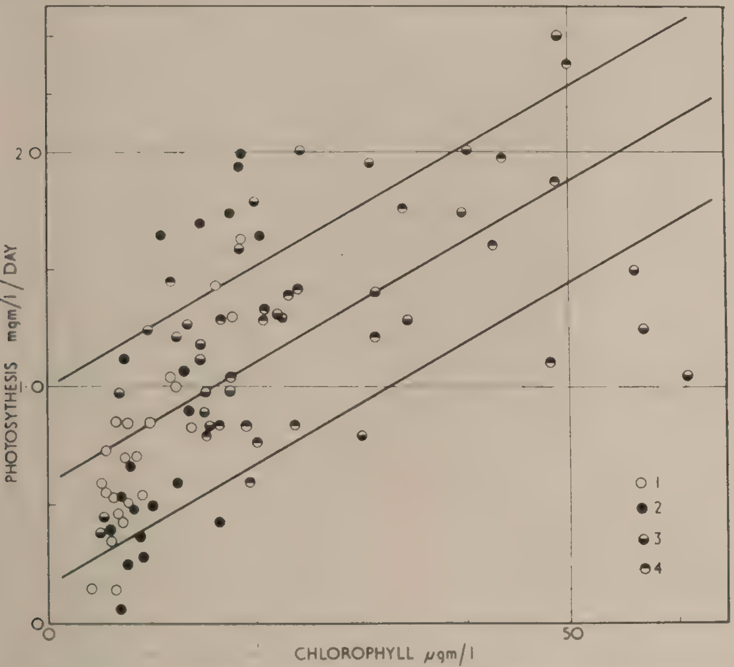

Fig. 2. Gross photosynthesis in the four tanks as a function of chlorophyll concentration. The centre line is the linear regression line and the others represent the standard error of estimate.

The maximum rate of photosynthesis was reached in five to twelve days after fertilization, and the rate then fluctuated with a general tendency to decrease. The two more heavily-fertilized tanks remained at a much higher level after the initial maximum was achieved.

VARIATIONS IN PHOTOSYNTHESIS

The large variations in photosynthesis may be attributed to variations in both population and environment. The relationship between rate of photosynthesis and some of the factors known to affect it was analyzed; much of the variation in photosynthesis turned out to be attributable to variations in chlorophyll, light, and phosphate concentration in the water. The details now follow.

During the time of the 1947 experiment, there were four periods during which relatively large levels of light were reached. The periods of greater photosynthesis tended to coincide with periods of high illumination; nevertheless, the coincidence is not perfect, and many variations in photosynthesis are not related to light (Fig. 1).

Obviously, the size of the population must be taken into account, since it showed large variations. The rate of photosynthesis per unit volume of water is the product of the population and the rate per unit of population. Even more pertinent to an explanation of the changes in photosynthesis is the amount of chlorophyll in the population (Fig. 1). After fertilization the population of phytoplankton increased greatly, and with it, chlorophyll. It is seen that the large amount of chlorophyll present in Tanks 3 and 4 during the period of time centred around July 20 partly compensated for the much lower light intensity relative to the period around July 13. The generally higher level of photosynthesis in Tanks 3 and 4 is matched by generally higher concentration of chlorophyll. The chlorophyll concentration in Tank 2 achieved a value only slightly more than that obtained in the 1946 experiment with the same amount of fertilizer in an unshaded tank, (erroneously recorded as mg/l in the 1947 paper).

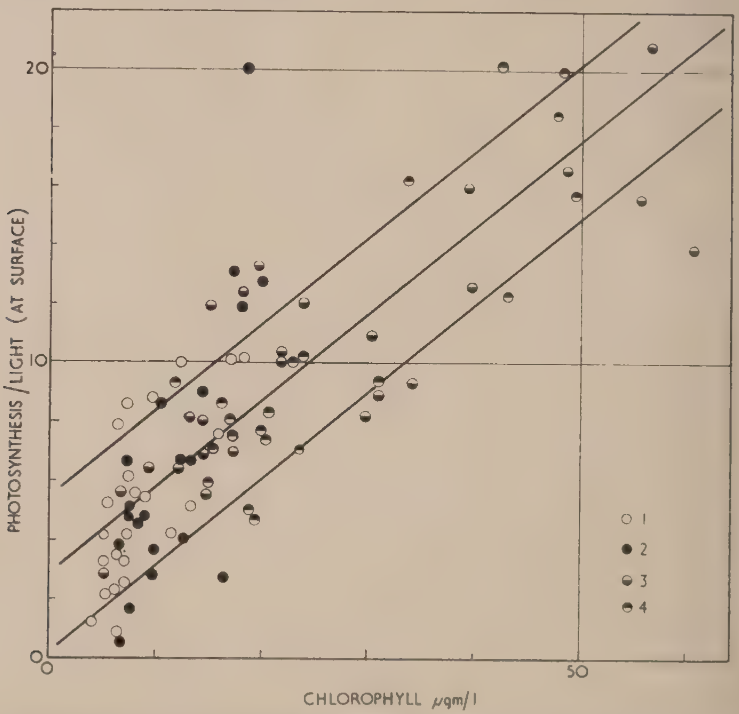

Fig. 3. Photosynthesis per unit of light as a function of chlorophyll concentration. The rates of photosynthesis shown in Fig. 2 have been divided by the mean light income (cal/cm^2/day) during the period of measurement, and the values multiplied by 1000.

The relationships just discussed are more clearly visualized if reference is made to correlation graphs (Figs. 2, 3, 4), in which consideration is limited to the 90 measurements made in the period before the re-fertilization on August 11. In the discussion which follows, the conventional correlation coefficient is designated as r_{4B}.

The following symbols will be used:

P	Gross rate of photosynthesis, as mg/l/day of oxygen
C	Chlorophyll concentration, as μg/l
L	Light at surface of tanks, cal/cm^2/min of visible light
L'	Light at mid-depth of tanks, same units
F	Phosphate concentration, μg at/l
P'	P/L
P''	P/L'
R	Rate of respiration of the population, mgm/l/day of oxygen
N	Net rate of photosynthesis, P–R

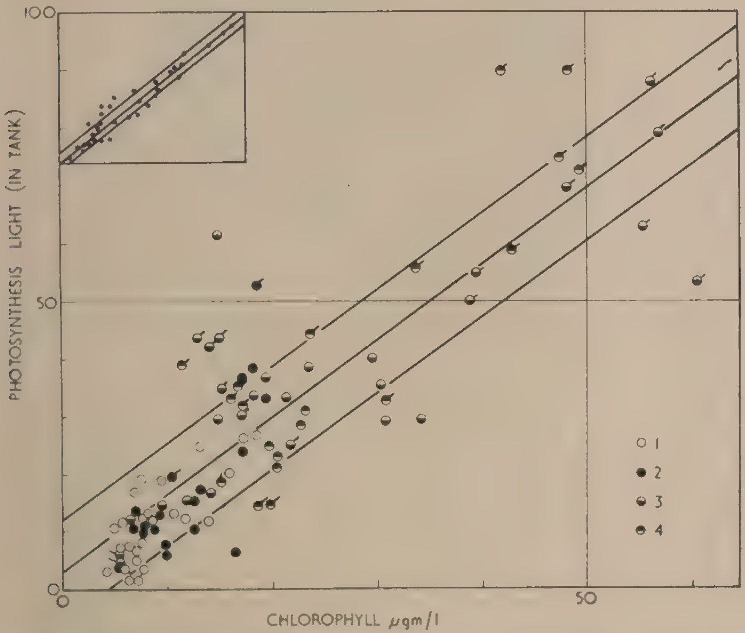

Fig. 4. As in Fig. 3, but the values of light used are those at a depth of 50 cm in the water. The points marked by lines are for periods when diatoms made up less than half the photosynthetic population by volume. The insert at the upper left is a copy of FLEISCHER's Fig. 7 (see text).

The simple relationship between photosynthesis and chlorophyll (Fig. 2) is seen to be rather low with a wide range of rate existing at all levels of chlorophyll concentration ($r_{PC} = 0{\cdot}64$). When each value of photosynthetic rate is divided by the corresponding light income, the degree of scatter is considerably reduced (Fig. 3) and the field of points is more nearly linear ($r_{P'C} = 0{\cdot}81$).

These coefficients show that, under the existing circumstances, a large part of the variation in photosynthesis is closely correlated with variations in but two factors known to have influence, chlorophyll and light, and suggest that chlorophyll was controlling more often than was light.

To give the results in a more complete numerically descriptive form, several linear regression equations were calculated. Of particular use in these equations is the standard error of estimate (S.E.E.) which, following SNEDECOR (1946, p. 117), can be used as a measure of dispersion of the points from the line of best fit, entirely analagous to the standard deviation in a frequency distribution.

It will be of interest to compare the standard errors of estimate of the regression equations with the standard deviation of the rate of photosynthesis, 0·545.

When photosynthesis is taken as a function of chlorophyll concentration alone (Fig. 2), the standard error of estimate is 0·420. When surface light intensity is added as a second independent variable, the standard error of estimate is reduced to 0·382 (Fig. 3). The equation relating these variables is $P = 0{\cdot}0172\mathrm{C} - 0{\cdot}0056\mathrm{L} - 0{\cdot}273$. Taking further account of the volume of plankton does not decrease variability, but taking account of phosphate concentration reduces the standard error of estimate still further to 0·283. In this analysis, phosphate concentration gives better results than does the rate of phosphate assimilation.

Thus, a large fraction of the deviation from the regression line can be accounted for statistically by variations in chlorophyll, light, and phosphate concentration. (Compare with RILEY, STOMMEL and BUMPUS, 1949.) The regression equation which relates these four variables-is:

$P = 0{\cdot}0304\mathrm{C} + 0{\cdot}0052\mathrm{L} + 0{\cdot}0275\mathrm{F} - 0{\cdot}239$ (S.E.E. 0·28). This equation describes the relationships which existed among the variables during the course of the experiment; but, on the basis of the known physical mechanisms involved, we can regard it additionally as a statement of relative effect of controlling factors.

The massive doses of phosphate which were added to the tanks do not represent usual concentrations available in natural conditions. Examination of the data shows that a positive relation with phosphate concentration existed only when the entire range of concentration was considered. Within the small range of variation of phosphate concentration usually met in natural waters, no correlation existed. Each tank behaved somewhat differently from the rest, and the relationships with phosphate concentration in the water are too complex for further discussion in this paper.

The light intensity to which reference has been made above is that at the surface of the water. Since the transparency of the water changed with the size of the population, the intensity to which the bottles were exposed is different, and not by a constant ratio. The intensity at a depth of 50 cm was calculated from measurements of transparency made by Mr. C. M. WEISS, and used in computing the points shown in Fig. 4, derived from Fig. 3. It is seen that, by taking account of the transparency of the water, the field of points is made more nearly linear and the regression line comes closer to the origin than in Fig. 3. The correlation coefficient $r_{P''C}$ is 0·86. While the difference from $r_{P'C}$ is not significant statistically, it is distinctly larger. The equation shown in the figure is:

$$P'' = 0{\cdot}735\mathrm{C} + 3{\cdot}057 \text{ (S.E.E. } 10{\cdot}72)$$

This treatment of the light data is something of an over-simplification, since it implies that there is a direct and linear correlation between rate of photosynthesis and light intensity. While the tanks were shaded to prevent inhibition by bright light, the sun was able to shine in during a small part of the day, and a simple proportionality is not to be expected. However, deviation is not serious, and a more detailed analysis of the available data is not justified. Nevertheless it should be realized that a more elaborate treatment of light might result in considerable reduction in the standard error of estimate. The relation of photosynthesis to light in natural aquatic populations has been reviewed in some detail by EDMONDSON (in press).

Because of considerations just discussed, and because certain influential factors were not measured, calculations were made to ascertain how much of the variation might have been eliminated by more rigorous control of conditions. Data published by FLEISCHER (1935) permit evaluation of variation when measurements of photosynthesis of pure cultures of *Chlorella sp.* were taken as a function of chlorophyll concentration under uniform environmental conditions. The amount of chlorophyll in the population was varied by raising the cells in media deficient in one of the nutrients; thus, in the example selected, the past history of the various cultures differed only in the concentration of iron in the medium in which the cells had grown. Otherwise, conditions were uniform, the cells of fairly uniform age being suspended in a standard medium for the measurement of photosynthesis under constant illumination and temperature. Despite the carefully controlled environment, and the presence of only one species, there was variation in the amount of photosynthesis accomplished by a given amount of chlorophyll. Some of FLEISCHER's series were somewhat less variable. Measurements made from FLEISCHER's Fig. 7 shows that the coefficient of correlation is 0·97. His data are plotted in the insert of Fig. 4, with which they may be directly compared. It has been shown that differences in the age of cultures of *Chlorella* make a difference in the effectiveness of chlorophyll, as do differences in the culture conditions. (EMERSON, GREEN and WEBB, 1940; WINOKUR, 1949; SARGENT, 1940). Thus, with material and conditions very much more uniform than in the tanks, there was a variability which was a relatively large part of that found in the tanks.

EFFECT OF TAXONOMIC COMPOSITION OF POPULATION

The analysis made above takes no account of the qualitative changes in the taxonomic composition of the populations. It might be expected that, as the specific composition of the plankton changed, there would be consequent changes in the photosynthetic rate for given amounts of chlorophyll and light. If so, there are two possibilities to discuss.

If the appearance or disappearance of particular forms were to make a large difference in the relationships under discussion, it might be argued that the largest differences would be made by changes in the representation of major taxonomic groups on the basis that, for example, any dinoflagellate is likely to be more like another dinoflagellate in its ecological requirements than a diatom.

There is a second possibility; that is, within each major taxonomic group there may be a wide variation in photosynthetic efficiency or ecological requirements from one species to the next. Thus, particular species of diatoms may be ecologically almost equivalent to particular species of dinoflagellates and different from other diatoms as far as photosynthetic effectiveness goes. Thus, replacement of a particular diatom by a dinoflagellate might not result in a measurable change in the relationships discussed, but replacement of the same diatom by another might result in a large change. Such adaptive radiation within the major groups is very probable, but data apparently do not exist to permit this question to be decided. There seem to be no comparative studies of the genera which were prominent in the tank populations comparable to WINOKUR'S (1948, 1949) work on eight species of *Chlorella*, and that stops short of a study of comparative nutrition.

Considerable effort was expended in trying to discern such qualitative sources of variation in the present data. As one approach, the fraction of the volume of phytoplankton material made up by diatoms was computed. This fraction varied from less than 1% to 97% by volume, with the other organisms being a great variety of kinds including dinoflagellates and *Chlorella*, but there was no discernible tendency for periods of large diatom content to be low or high in the amount of photosynthesis per unit light and chlorophyll. The periods during which the population was composed of less than 50% diatoms are indicated by lines attached to the points of Fig. 3. Thus, large variations in the representation of diatoms did not alter the relationships discussed. Likewise there was no relation with the fraction of the population made up by non-photosynthetic protista. This is not to say that many aspects of population biology will not be altered by taxonomic changes of this kind, or that such phenomena did not exist during the tank experiments, but merely that the relation of photosynthesis to chlorophyll and light depended more on the sheer quantity of chlorophyll than on the way the chlorophyll was distributed among the major taxonomic groups present.

PHOTOSYNTHETIC POPULATION EFFICIENCY

Having measurements of the rate of energy input into the tanks and the gross rate of photosynthesis, we can calculate the gross population efficiency, or fraction of energy used in photosynthesis. In Experiment 1, gross efficiency for the four tanks together was 0·34% when computed on the basis of surface intensity of visible light, and 0·95% on the basis of the intensity of the depth of the bottle. The figures for each tank are in order, for surface intensity, 0·23, 0·31, 0·41. and 0·43%. For intensity at the depth of the bottles, the corresponding figures are 0·51, 0·67, 1·29, and 1·56%.

Since these figures are based on the intensity of visible light, they should be multiplied by 2 before comparing them with figures in the literature which are based on total radiation. Efficiencies of natural, unfertilized populations have been reported between 0·02 and 0·40%. NELSON and EDMONDSON (in press) discuss a lake the efficiency of which was greatly increased by fertilization. That the heavily fertilized tanks are not much more efficient relative to natural populations may be surprising, but is easily explained by the fact that the tanks were so shallow that much of the avaliable light must have been wasted by absorption into the sides and bottom and by reflection back out of the water. That fertilization increased efficiency can best be seen by comparing each tank with Tank 1, bearing in mind that Tank 1 was inadvertently fertilized lightly.

ASSESSMENT OF CONDITION BY ENRICHMENT

As shown in previous sections, the responsiveness of different populations to fertilization was different, and varied with the amount of fertilizer. For full interpretation of events in natural populations, it is necessary to obtain information on responsiveness in order to identify limiting and controlling factors. The work of LUND on lakes is the most successful to date, basing interpretation of seasonal events on laboratory analysis of the physiological condition of the population and its response to changed conditions (1949, 1950).

In the present work, a number of enrichments were made with nutrients added to the bottles, not the whole tanks, in order to determine the degree to which these substances might be limiting photosynthesis.

For example, on July 29 the population of Tank 2 was highly responsive to enrichment with phosphate and nitrate, while that of Tank 4 showed no response (Table II). The results are interpretable on the basis that Tank 4 had previously been more heavily fertilized, relative to Tank 2, and the population of the former tank was not inhibited by lack of nutrients. The phosphate concentration in the two tanks before enrichment was 0·13 and 0·46 μg at/1 of P, respectively.

Table II

Results of enrichment with nutrients, July 29–31 1947. The rate of photosynthesis is tabulated for bottles enriched with phosphate, nitrate, both, and nothing

	Photosynthesis in	
	Tank 2	*Tank* 4
Added:		
O (control)	0·6 mg/1/day	0·9
P (0·5 μg/1)	0·7	0·9
N (80 μg/1)	1·1	0·9
P and N	1·3	0·9

PHOTOSYNTHESIS AND PHOSPHATE ASSIMILATION

Previously, it was demonstrated that there was a close correlation between amount of oxygen produced by a population and amount of phosphate removed from the water (EDMONDSON and EDMONDSON, 1947). This relation was investigated further in the present work. In Experiment 3, phosphate assimilation was measured in a manner analogous to that by which photosynthesis was measured, by measuring the phosphate concentration in suspended bottles. In most series, phosphate increased in the dark bottle and decreased in the light bottle. By subtracting the change in the dark bottle from that in the light bottle, one obtains a gross phosphate assimilation which, in most cases, is a negative number, indicating decrease of concentration in the water. Similarly, the changes in particulate phosphorus were measured. The data on phosphorus were taken by Dr. DAVID M. PRATT, who made a detailed study of the phosphorus cycle in Experiment 3 (PRATT, 1950); his paper should be consulted in connection with this section. It is of interest to compare assimilation of phosphorus with the measurements of photosynthesis.

The phosphate which appears as net change in the dark bottle is most likely released by bacteria and animals, not by intact algae. It would seem, therefore, that in addition to comparing the gross changes in phosphorus with gross photosynthesis, it would be meaningful also to study the relation between gross phosphate assimilation and net photosynthesis, where the latter is the rate of change of oxygen in the light bottle, and is equivalent to the quantity (gross photosynthesis–respiration). That it is reasonable to study this relation is shown by considering the fact that carbon dioxide but not phosphate is freely released by algae in the dark bottle. Unfortunately, with present techniques, a true measurement of net photosynthesis is not obtained, since a large population of bacteria develops on the glass surface of the bottle. Thus, the rate of respiration and presumably phosphorus metabolism is higher in the bottle than in the relatively unconfined population of the tank. Nevertheless, under the circumstances which existed, the bacterial population is probably similar in the two bottles. Plate counts differed little. Thus, the difference between the bottle population and the tank population is that the former had a higher proportion of bacteria. Any relation which would depend upon the ratio of bacteria to other organisms would be modified. (See RYTHER, 1954).

Both the rate of disappearance of phosphate from the water and the rate of increase of phosphorus in particulate form (organisms) showed a rather close relation with net photosynthesis and with gross photosynthesis. In the latter measurements, there were three pairs of points which diverged greatly from the general pattern, because of a high rate of photosynthesis not matched by the high rate of phosphorus uptake (Fig. 5). The reason for the divergence of the aberrant points is not evident. The data are for determinations made toward the end of the period of investigation, and the rate of respiration was unusually high. It is possible that photosynthesis was able to proceed rapidly, without a corresponding uptake of phosphate, because of phosphorus stored in the cells (KETCHUM, 1939).

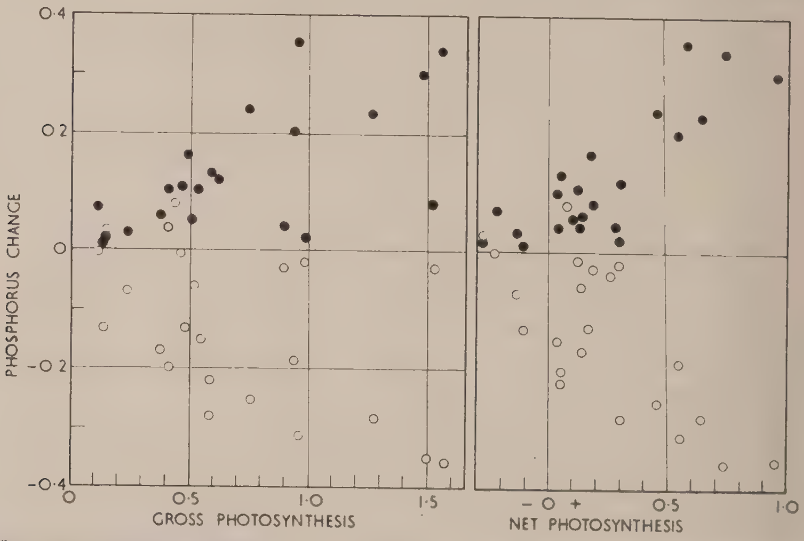

Fig. 5. Rate of change of phosphorus as a function of gross photosynthesis (left) and net photosynthesis (right) in Experiment 3. Particulate phosphorus is shown by filled circles and phosphate phosphorus by open circles. The rate of change of phosphorus is given as μgm at/1/day., photosynthesis as before.

In both cases, the rate of increase of particulate phosphorus very closely matches the rate of decrease of phosphate in the water. Individual pairs may not match well because phosphorus can be lost from the particulate fraction without immediately appearing as phosphate, but the fields of points do match.

DISCUSSION

The investigation partially summarized in this paper was intended primarily to explore certain problems of aquatic productivity. The ideas discussed concern freshwater as well as marine populations. Extrapolation from pure culture work to natural populations is complicated by the existence of many phenomena which do not operate in one-phase, single-species cultures, and which may be exceedingly difficult to duplicate in ordinary laboratory conditions. While the large outdoor tanks do not provide the elegance of complete environmental control available in the laboratory, they permit some control, as well as a degree of simplification not available in natural shallow habitats, in which the mud-water interface makes complications. They proved to be very useful in providing a large, manipulable environment, intermediate between laboratory cultures and natural bodies of water, from which large samples could be withdrawn without seriously depleting the population. They may profitably be used in the problem of interpreting natural situations, and in designing efficient programs of experiments with controlled conditions.

One of the pressing problems is to establish relationships among the various population functions which are involved in biological production. Of these, the relation of photosynthetic rate to amount of chlorophyll present, and the degree to which this relation may be modified by various environmental conditions, has been discussed at length. The ecological position of chlorophyll is obvious, but critical studies must be continued before much useful prediction from measurements of chlorophyll can be made. A second problem of interest is that of the interrelations among photosynthesis, population growth, and nutrient uptake. It must be expected that in general these functions will be related, and measurements of one will give information about others which may in some situations not be measurable directly. Finally, further development of methods of evaluating the extent to which various factors are limiting production at any moment should lead to greater understanding of the general problem of productivity.

REFERENCES

Edmondson, W. T. and Edmondson, Y. H. (1947), Measurements of production in fertilized salt water. *J. Mar. Res.*, **6,** 228–245.

Edmondson, W. T. (in press), The relation of photosynthesis by phytoplankton to light in lakes. *Ecology.*

Emerson, R., Green, L. and Webb, J. L. (1940), Relation between quantity of chlorophyll and capacity for photosynthesis. *Plant Physiol.*, **15,** 311–317.

Fleischer, W. E. (1935), The relation between chlorophyll content and rate of photosynthesis. *J. Gen. Physiol.*, **18,** 573–597.

Gaarder, T. and Gran, H. H. (1927), Investigation of the production of plankton in the Oslo Fjord. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer,* **42,** 1–48.

Hutchinson, G. E. (1941), Mechanism of intermediary metabolism in stratified lakes. *Ecol. Monogr.*, **11,** 21–60.

Jenkin, P. M. (1937), Oxygen production by the diatom *Coscinodiscus excentricus* in relation to submarine illumination in the English Channel. *J. Mar. Biol. Assoc., U.K.*, **22,** 301-342.

Ketchum, B. H. (1939), The absorption of phosphate and nitrate by illuminated cultures of *Nitzschia closterium. Amer. J. Bot.*, **26,** 399–407.

Ketchum, B. H. (1939), The development and restoration of deficienceis in phosphorus and nitrogen composition of unicellular plants. *J. Cell. Comp. Physiol.*, **13,** 373–381.

Lund, J. W. G. (1949), Studies on *Asterionella.* I. The origin and nature of the cells producing seasonal maxima. *J. Ecol.*, **37,** 389–419.

Lund, J. W. G. (1950), Studies on *Asterionella formosa* Hass. II. Nutrient depletion and the spring maximum. Part I. Observations on Windermere, Esthwaite Water and Blelham Tarn. *J. Ecol.*, **38,** 1–14.

Manning, W. M. and Juday, R. E. (1941), The chlorophyll content and productivity of some lakes in Northern Wisconsin. *Trans. Wisconsin Acad.*, **33,** 363–393.

Nelson, P. R. and Edmondson, W. T. (in press), Limnological effects of fertilizing Bare Lake, Alaska. *U.S. Fish and Wildlife Serv., Fish. Bull.*

Pratt, D. M. (1950), Experimental study of the phosphorus cycle in fertilized salt water. *J. Mar. Res.*, **9,** 29–54.

Riley, G. A., Stommel, H. and Bumpus, D. F. (1949), Quantitative ecology of the plankton of the Western North Atlantic. *Bull. Bingham Oceanogr. Coll.*, **12** (3), 1–169.

RYTHER, J. H. (1954), The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. *Deep-Sea Res.*, **2**, 134–139.

SARGENT, M. C. (1940), Effect of light intensity on the development of the photosynthetic mechanism. *Plant Physiol.*, **15**, 275–290.

SNEDECOR, G. W. (1946), Statistical methods. Ames, Iowa, 4th Ed., xvi 485 pp.

WHIPPLE, G. C. (1896), Some experiments on the growth of diatoms. *Technology Quarterly*, **9**, 145–168.

WINOKUR, M. (1948), Growth relationships of *Chlorella* species. *Amer. J. Bot.*, **35**, 118–129.

WINOKUR, M. (1948), Photosynthesis relationships of *Chlorolla* species. *Amer. J. Bot.*, **35**, 207–214.

WINOKUR, M. (1949), Aging effects in *Chlorella* cultures. *Amer. J. Bot.*, **36**.

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Die Ausbreitung des Mittelmeerwassers im Nordatlantischen Ozean

By A. DEFANT

Summary—The spreading of Mediterranean water flowing out through the Straits of Gibraltar into the open Atlantic is essentially a pure mixing process. This process is significant in the formation of oceanic water masses in the open ocean.

DER AUF das thermo-haline Kräftesystem beruhende Wasseraustausch zwischen den grossen Nebenmeeren und dem freien Ozean durch die sie verbindenden Meeresstrassen hat sich für die Tiefenzirkulation der grossen Ozeane als höchst wirksam erwiesen. Die schweren Wassermassen aus den grossen subtropischen Nebenmeeren, wie es das Europäische Mittelmeer und das Rote Meer sind, ergiessen sich in den Ozean, wenn sie die Mündung der Meeressstrasse in den freien Ozean verlassen haben. Infolge des hohen Salzgehaltes sind sie schwerer als jene Wassermassen, die im freien Ozean in der Mündungstiefe des Unterstromes aus dem Mittelmeer lagern. Dadurch erhalten sie eine sinkende Tendenz und folgen dem Prinzip der stratosphärischen Zirkulation, nämlich absinkend sich jene Tiefenschicht auszusuchen, die ihrer Dichte entspricht. Hier breiten sie sich dann unter ausgedehnten Vermischungsvorgängen auf isopyknischen (isentropen) Flächen, im wesentlichen also horizontal aus. Durch Verfolgung des Salzgehalts-maximums, das den eindringenden Wassermassen eigen ist, lässt sich der Weg angeben, den diese Wassermassen bei ihrer Ausbreitung und Vermischung nehmen. Klarer als durch die Linien gleichen Salzgehaltes in dieser Kernschichte des Mittelmeerwassers vor der Strasse von Gibraltar lässt sich die Ausbreitung des Mittelmeerwassers im Atlantischen Ozean vor der Mündung der Gibraltarstrasse nicht zeigen (Abb. 1). G. WÜST hat im "Meteor "-Werk eine vollständige Bearbeitung der vorhandenen ozeanographischen Reihenmessungen durchgeführt und in zwingender Weise den Nachweis erbracht, dass für das obere nordatlantische Tiefenwasser die durch die Strasse von Gibraltar im Unterstrom in den Atlantischen Ozean eindringenden salzreichen und warmen Mittelmeerwassermassen weitaus die Hauptquelle bilden. In den spanischen Gewässern vor der Meeresstrasse breitet sich das Mittelmeerwasser in etwa 1000 bis 1100 m Tiefe radial nach allen Seiten aus, verliert hierbei seinen hohen Salzgehalt und seine hohe Temperatur durch Vermischung mit den Wassermassen, zwischen denen es sich ausbreitet. WÜST hat gezeigt, dass die Mittelmeerwasserart gegen den Südatlantischen Ozean allmählich auf 2000 m absinkt, aber schon am Aequator ist diese Wasserart nur noch mit 20 bis 10 Prozent im Aufbau der dort lagernden Wassermassen vorhanden. Die Abb. 1 zeigt eindrucksvoll die Reichweite der unmittelbaren mittelmeerischen Beeinflussung nördlich von 15° N und der mittelbaren südlich davon durch den nach Süden gehenden nordatlantischen Tiefenstrom.

Ganz ähnlich sind die Verhältnisse im nördlichen Indischen Ozean, wo der Ausfluss des sehr salzreichen Wassers aus dem Roten Meer durch die Strasse von Bab el Mandeb sich weit in den Arabischen Golf und noch weiter gegen Süden im Indischen Ozean bemerkbar macht. Hier steht allerdings keine solche genaue Untersuchung der Verhältnisse im Raum, wie bei der Strasse von Gibraltar zur Verfügung, aber die Längsschnitte, die vom Golf von Aden ausgehend durch den Indischen Ozean gelegt sind, zeigen die Zunge hohen Salzgehaltes, die von der Strasse von Bab el Mandeb aus sich weit nach Osten und später nach Südosten ausbreitet.

Es mag erstaunlich erscheinen, dass die Wassermassen, die durch die relativ engen Strassen von Gibraltar und Bab el Mandeb hinausfliessen, einen so grossen Einfluss auf die Zusammensetzung und die ozeanische Zirkulation der Wassermassen der freien Ozeane unterhalb 1000 m Tiefe haben sollen. Aber schon eine kleine Ueberschlagsrechnung zeigt, dass dies tatsächlich durchaus möglich ist, ja zu erwarten ist.

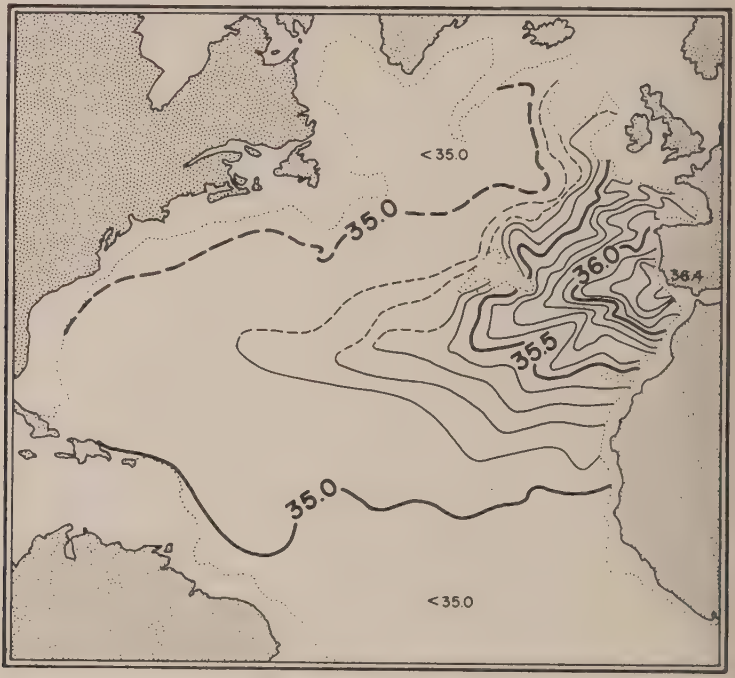

Abb. 1. Die Ausbreitung und Tiefenlage der Kernschicht des Mittelmeerwassers im Atlantischen Ozean (intermediäres Salzgehaltsmaximum).

Aus dem Mittelmeer fliessen durch die Strasse von Gibraltar pro Jahr rund 52,000 km³ Mittelmeerwasser in den Atlantischen Ozean. Nimmt man als ungefähre mittlere Ausbreitungsgeschwindigkeit im Ozean etwa 4 cm/sek, dann würde ein Wasserteilchen in sechs Jahren bis auf die Höhe von Buenos-Aires-Kapstadt (etwa 35° S Br.) gelangen. In diesen 6 Jahren liefert die Strasse von Gibraltar 312,000 km³ Mittelmeerwasser, das sich über die ganze Wassermasse bis in diese Breiten verteilt. Nimmt man an, dass die Verteilung *gleichformig* auf die Schicht von 500 m Mächtigkeit von 45° N bis 35° S Br erfolgt, so ergibt sich immerhin eine mittlere Beimengung von rund 1·2 Prozent Mittelmeerwasser. Die Schichten der Spanischen Bucht werden natürlich viel mehr Prozent aufweisen, jene weiter im Süden viel weniger; aber man erkennt, welch bedeutenden Einfluss auf diese Weise die subtropischen Nebenmeere auf die

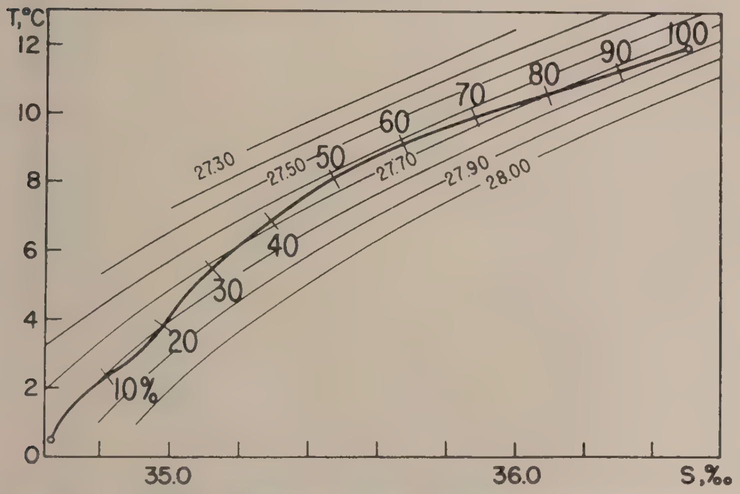

Abb. 2. $S = f(T)$ — Kurve der Beziehung zwischen Temperatur und Salzgehalt in der Kernschicht des Mittelmeerwassers im Atlantischen Ozean (nach WÜST).

ozeanische Zirkulation in den Tiefen der Ozeane gewinnen. WÜST hat mittels der $S = (T)$-Methode in eingehender Weise den prozentuellen Anteil des Mittelmeerwassers am Aufbau der Wassermassen des Atlantischen Ozeans ermittelt und in Abb. 2 gezeigt, wie allmählich dieser Anteil von 100 Prozent in der Strasse von Gibraltar auf 20 Prozent in 10° N bis 0° Br. herabgeht, indem durch die Vermischung mit anderen Wasserarten eine allmähliche Herabsetzung der Mittelmeeranteils stattfindet. Die Abb. 1 zeigt in zwingender Weise, dass dieser Vorgang der Vermischung

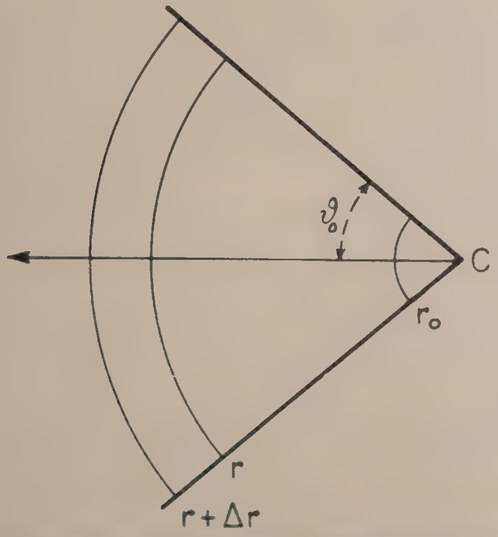

Abb. 3. Modell zur Erfassung der Ausbreitung eines Einschubes salzreichen Wassers bei C.

vor der Strasse von Gibraltar ein *Austauschproblem* ist. Es kann in einfacher Weise in einem Modell etwa folgenderweise beschrieben werden.

Die Mündung eines Nebenmeeres in den freien Ozean kann als eine Salzquelle angesehen werden, deren Ergiebigkeit vom Wasseraustausch zwischen den beiden Meeren abhängt. Die aus der Mündungsstrasse ausfliessenden Wassermassen breiten sich auf Isentropenflächen im freien Ozean aus, wobei eine ständige Vermischung mit den Wassermassen der Umgebung stattfindet. Die Salzquelle befinde sich im Punkte C und die anschliessenden Küsten bliden dort den Winkel $2\theta_0$ (siehe Abb. 3). Die Entfernung eines Punktes auf einer Isentropenfläche von C sei r; die ausschliesslich *radiale* Grundgeschwindigkeit ist dann $v=dr/dt$. Die Strombahnen der Wasserausbreitung divergieren also vom Punkte C aus. Betrachtet man ein Volumelement des ringförmigen Sektors r und $r + \triangle r$, dann müssen sich in ihm bei *stationären* Verhältnissen die Advektion der Salzmenge und die Ausbreitung durch turbulente Vermischung das Gleichgewicht halten. Dies führt in bekannter Weise zur Beziehung

$$\frac{A}{\rho}\frac{\partial^2 S}{r^2 \partial .^2} - \frac{\partial (vrS)}{r\partial r} = 0 \tag{1}$$

wenn nur die seitliche Vermischung mit dem Austauschkoeffizienten A Berücksichtigung findet. Die Kontinuitätsgleichung verlangt, dass

$$\frac{\partial vr}{\partial r} = 0 \tag{2}$$

ist, oder $v.r = \text{const.} = r_0 v_0$, wenn v_0 und r_0 sich auf einen beliebigen Anfangssektor in der Nähe von C beziehen. Setzt man $r = a\xi$ und $r_0 = a\xi_0$, so hat mit der Beziehung (2) die Differentialgleichung (1) eine Lösung in der Form

$$S = f(\theta).\quad F(\xi), \tag{3}$$

wobei man auf die Grenzbedingung $f(\theta) = 0$ für $\theta = \pm\,\theta_0$ zu achten hat. Aussserdem soll $S = S_0 + \delta_0$ für $\xi = \xi_0$ und $\theta = 0$ sein. Dann wird aud (3):

$$S = S_0 + \delta_0 \left(\frac{\xi_0}{\xi}\right)^\beta \cos\frac{\pi}{2\theta_0}. \tag{4}$$

worin

$$\beta = \frac{\pi^2}{4\theta_0^2}\cdot\frac{A}{\rho v a \xi_0} \tag{5}$$

ist.

Die Lösung lässt sich durch eine Fourier'sche Entwicklung des Anfangszustandes auf den Ausgangssektor r_0 beliebig verallgemeinern.

Die Anwendung dieser theoretischen Ableitungen auf den vorliegenden Fall vor der Strasse von Gilbraltar und der Ausbreitung des Mittelmeerwassers vor dieser im freien Ozean ergibt folgende Berechnungen. S_0 ist gemäss der Beziehung (4) der Salzgehalt in grosser Entfernung von C und man hat, wenn man der Einfachheit halber nur die Verhältnisse bei $\theta = 0$ betrachtet:

$$S_{r_0} = S_0 + \delta_0 \quad \text{und} \quad S_r = S_0 + \delta_0 \left(\frac{\xi_0}{\xi}\right)^\beta \tag{6}$$

Daraus folgt:

$$\frac{S_r - S_0}{S_{r_0} - S_0} = \left(\frac{\xi_0}{\xi}\right)^{\beta} \tag{7}$$

Die Grössen auf der linken Seite lassen sich aus den Beobachtungstatsachen als Funktion von ξ ableiten, sodass die Möglichkeit besteht, Beobachtungen und Theorie miteinander zu vergleichen. Den Anganfssektor wollen wir in $r_0 = a\xi_0 =$ 320 km vom Querschnitt Trafalgar—Tanger am Westrand der Gibraltarstrasse setzen. Aus einer grösseren Zahl von strahlenformig von der Mitte dieses Querschnittes ausgehenden Kurven wurde aus der Abb. 1 die Entfernungen der in ihr eingetragenen Isohalinen vom Ausgangsquerschnitt bestimmt und aus allen diesen Werten auf graphischen Wege eine mittlere Verteilung von S in Abhängigkeit von r abgeleitet. Die folgende Tabelle gibt diese Werte von S für die einzelnen $\Delta r = r - r_0$. Die Grösse S_0 lässt sich zu 34·95°/₀₀ ansetzen, sodass

$$S_{r_0} - S = 1{\cdot}50$$

Tabelle I

Δr km	S °/₀₀	$\frac{S_r - S_0}{S_{r_0} - S_0}$ %	$\frac{\xi_0}{\xi}$	$\left(\frac{\xi_0}{\xi}\right)^{0\cdot65}$ %
0	36·45	99	1	100
200	36·20	82	0·615	74
400	35·90	62	0·444	59
600	35·80	56	0·348	51
800	35·68	48	0·286	45
1000	35·58	41	0·242	40
1200	35·54	39	0·210	37
1400	35·48	35	0·186	34
1600	35·45	33	0·167	32
1800	35·43	32	0·151	30
2000	35·38	28	0·138	28
2200	35·30	23	0·127	27
2400	35·29	22	0·118	25
2600	35·29	22	0·110	24
2800	—	—	0·102	23
3000	35·30	23	0·096	22
3200	—	—	0·091	22
3400	—	—	0·086	21
3600	35·25	20	0·082	20
3800	—	—	0·078	20
4000	35·20	17	0·076	19

wird. Damit können die in der Tabelle stehenden Werte von $\frac{S_r - S_0}{S_{r_0} - S_0}$, ausgedrückt in Prozenten des Anfangswertes, ermittelt werden, Die Werte $\frac{\xi_0}{\xi}$ ergeben sich aus $\frac{r_0}{r_0 + \Delta r}$; auch sie stehen in obiger Tabelle. Bildet man $\left(\frac{\xi_0}{\xi}\right)^{\beta}$ mit $\beta = 0{\cdot}65$, so findet man, wie die Tabelle zeigt, eine sehr befriedigende Uebereinstimmung mit den aus den Beobachtungen abgeleiteten Werten. Abb. 4 gibt diesen Vergleich zwischen Beobachtung und Theorie und zeigt, dass die theoretischen Grundlagen durch die Beobachtungen völlig bestätigt werden. Eine bessere Uebereinstimmung hätte sich bei anderer Wahl des Zahlenwertes von β nicht erzielen lassen.

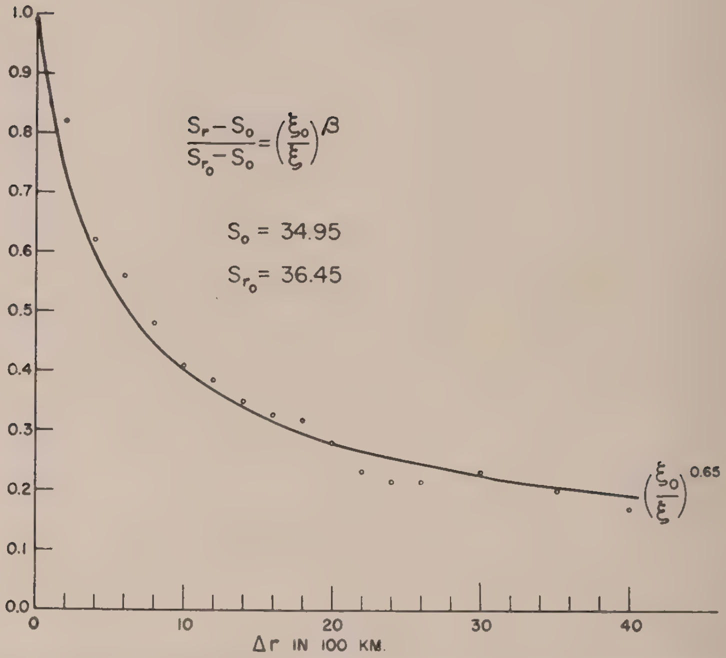

Abb. 4. Die Ausbreitung des Mittelmeerwassers im Atlantischen Ozean vor der Strasse von Gibraltar. —— nach der Theorie, ∘ ∘ ∘ nach den Beobachtungen.

Nun zeigt die geographische Karte des Gebietes vor der Strasse von Gibraltar, dass $2\theta_0$ zu ungefähr 130° anzusetzen ist; dies ergibt $\left(\frac{\pi}{2\theta_0}\right)^2 = 1{\cdot}9$ und mit $r_0 = a\xi_0 = 3{\cdot}2 \times 10^7$ cm wird aus der Definitionsgleichung für β : $\frac{A}{\rho v} = 1{\cdot}1 \times 10^7$ cm. Man erhält also auch hier, wie es sonst bei ähnlichen Berechnungen der Fall ist, nur das Verhältnis des Austauschgrösse zur Grundgeschwindigkeit. Nimmt man letztere zu etwa $v_0 = 5$ cm/sek an, so wird $A/\rho = 5{\cdot}5 \times 10^7$ cm²/sek. Dieser Wert für den seitlichen Austauschkoeffizienten fügt sich in bester Weise in die Reihe der Bestimmungen dieser Grösse aus ganz anderen Strombedingungen (siehe SVERDRUP, JOHNSON and FLEMING, 1942, p. 485; oder PROUDMAN, 1953, p. 120 u.f.).

Die Vorgänge der Ausbreitung des aus der Strasse von Gilbralter ausfliessenden Mittelmeerwassers in den freien Atlantischen Ozean sind somit im wesentlichen ein reiner Vermischungsvorgang und man erkennt, welche Bedeutung diesen Prozessen für den Aufbau der ozeanischen Wassermassen im freien Ozean zukommt.

Innsbruck, April 1955.

LITERATUR

PROUDMAN, J. (1953), *Dynamical Oceanography*. London, Methuen & Co., Ltd., 409 pp.
SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. H. (1942), *The Oceans: their Physics, Chemistry, and general Biology*. New York, Prentice-Hall, Inc., 1087 pp.

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New directions in fishery research

By Lionel A. Walford

The Fishes of the Gulf of Maine, by Bigelow and Schroeder, published two years ago, brings up to date a work that has been an American ichthyological classic for 30 years. It sums up our knowledge about every species of the northwest Atlantic that regularly occurs in the oceanic bight from Nantucket Shoals and Cape Cod eastward to about 65° W. longitude and including the Bay of Fundy. When read in comparison with the 1924 edition, it measures the progress which biologists have been making in their studies of fishes in this area. In bringing together the work of three generations, it marks where we are now, and serves as a basis on which to consider the question of where to go from here. In the following paragraphs, I propose to examine some facets of this question from the viewpoint of fishery research.

In general, the ichthyological fauna of the North Atlantic is now fairly well known; at least the species which are of actual or potential commercial interest are well known. This does not mean that taxonomy is finished in the Gulf of Maine (or anywhere else for that matter) leaving only the routine job of keeping the bottles on the museum shelves properly labelled and filled with alcohol. What has been done so far is to lay the foundation on which the taxonomy of the future must be built; for there remains the enormously important and difficult work of clarifying conceptions of the sub-populational structure of the species. This is not of " mere academic interest ", as people who are unsympathetic to this line of research sometimes scornfully assert. Fishery investigators have everywhere shown it to be a fundamental necessity; for sub-populations often differ enough from each other in many ways—in rates of growth and mortality, in fecundity, in migratory habits, and in various other biological characteristics, that these segments of species must be studied, fished and regulated as distinct entities.

No matter how distinct they may be genetically, however, they are exceedingly difficult to define, for body proportions and meristic counts vary widely within sub-populations; they overlap broadly between populations; and they are affected by the continually varying conditions of the environment, particularly temperature. Because of the consequent limitations in the usefulness of anatomical features, other means of identifying sub-populations are being sought in the fields of biochemistry, serology, parasitology, and experimental marking. Whatever methods be used for analysing sub-populations, it is necessary to systematically sample large quantities of fish throughout the range of each species under study. In the northwest Atlantic, this laborious and costly work has hardly begun. So far, it has necessarily been concentrated on only the species of greatest commercial importance, namely haddock, cod and red-fish; and even these few species have been studied intensely only over a part of their total distributions. Thus, the study of sub-populations of these must continue, while that of all the other species still lies ahead.

The Fishes of the Gulf of Maine is full of information that is best classed as Natural History. There is much more of this than could be assembled for other parts of North

America, since history is longer and the facilities for keeping records go back further there; universities and museums are more ancient, great fisheries and fishery researches have been longer established, and there has been more opportunity to observe the habits of fishes and to record the vagaries of fisheries there than in other sections of the country. Thus over the course of over 300 years there has accumulated a great store of knowledge about western north Atlantic fishes—about the characteristics of their environment, their seasons and places of spawning, the structure of their eggs and larvae, their food habits, routes of migrations, anomalies of occurrences, and many other matters relating to normal patterns of life history and to the deviations therefrom.

Natural History has been unappreciated for a long time, and is now at last again coming into its own, though perhaps under a different label. During the 1920's and 1930's the extraordinary growth of new fisheries such as for haddock in New England, for sardines in California, and for shrimp in the Gulf of Mexico, aroused concern for the future productivity of those natural resources that were being subjected to unprecedented exploitation. It was logical that these fisheries should be regulated as promptly as possible in order to safeguard them from extermination, and that to be effective, the regulations must be based on scientific information. It transpired from preliminary inquiries that a special kind of information was required which in fact did not exist. Although there was a large store of facts, none of it was suitable for calculating estimates of the sizes and ages at most profitable capture. Under the impetus of the demands of the time, therefore, biologists whose interests might otherwise have been natural history took up the study of fishery biology. At first they were preoccupied with determining the effect of fishing on the abundance and productivity of populations of fish. For this they paid the bulk of their attention to founding useful systems of commercial statistics and to the analysis of the quantities, sizes and ages of fish caught in relation to the amount of effort required in the catching. They tended to limit biological studies to those features of life history required for scientific regulation, i.e. rates of growth, death and replacement.

Fishery research might have remained so for a much longer time had it been proved unequivocally that fishing alone causes depletion, which can always be corrected simply by controlling the catch. However, one of the principal results of studies over the past 30 years has been to bring out that, although fishing certainly does affect the abundance of fishes, so also do events which happen in the ever changing environment. Long period trends in climate and hydrography, for example, affect distribution and abundance of all species, whether they are fished or not; and they affect different species in different ways. Thus there is continuous change in the numerical interrelations among the many species inhabiting an environment, perhaps with some kind of pattern of oscillations which has yet to be deciphered.

Fishery researchers had first thought to speed their progress towards practical results by limiting the scope of their studies to the species of greatest importance and to the problems of greatest urgency. Every study about those species, however, has made it more evident that they can not be understood out of context from the intricate system of their biological environment composed by their predators (including man), their competitors and their prey. So it is that fishery researchers have been finding it necessary to rediscover natural history (now called ecology), and to enlarge the scope of their programmes in order to establish a proper balance between studies of fisheries and of fishes. The average fishery programme of today is neither a one-man nor a one-agency enterprise. It generally involves the collaboration of several institutions, sometimes of several nations, and the participation of many scientists having among them a wide variety of disciplines and talents.

Most fishery investigations begin with the tacit hope that a solution to what had looked like a clear-cut problem will be reached, and the work concluded in five or six years. Of course this never happens. Research about the effect of varying exploitation upon irregularly oscillating populations of fishery organisms can not be concluded for all time any more than can research about any other constantly changing natural phenomena. In this connection, it might be helpful in our thinking to alter our concept of the dimensions of time from years to generations. The time required for a brood of fishes to reproduce itself (i.e. a generation) varies from one species to another, but commonly runs about three to eight years. To formulate dependable principles about fishes, it is necessary to follow many generations. Most fishery problems also involve human affairs. Those that concern us now will probably be much more acute a generation hence (i.e. 30 years from now) when people will be more numerous and their food needs consequently greater.

Thus the new directions in fishery research are towards greater comprehensiveness —the whole of species with all their sub-populations; the whole of environments with all their component species. This takes up again the tradition established far back in the past, which is behind books like *Fishes of the Gulf of Maine*, and promises to carry it forward to further enrich human knowledge about the sea.

REFERENCES

Bigelow, Henry B. and Schroeder, William C. (1953), Fishes of the Gulf of Maine. *Fishery Bull.* 74, *Fish. Bull., Fish and Wildlife Serv.*, **53**, 1–560, 288 text figs.

Bigelow, Henry B. and Welsh, William W. (1924), Fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40**, 1–550, 278 text figs.

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Coastal currents and the fisheries *

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THE WATERS over the continental shelf from Labrador to Cape Hatteras have been examined and described many times over the last 40 years or so. Certain characteristic features of the distribution of temperature and salinity are to be found along this whole stretch of coastline. Here many clear-cut examples of the basic problems of the circulation of coastal waters are to be encountered, yet it cannot be claimed that much additional understanding has been gained since the pioneer studies of BIGELOW (1927; 1933).

When the present writer was a graduate student at Harvard, Dr. BIGELOW had reached the conclusion that significant advancements in marine biology would in all probability have to await a much better understanding of the circulation of the ocean. He planned his own work, and also the early programme of the Woods Hole Oceanographic Institution, accordingly. After 25 years, the best that can be said is that we have gained a clearer picture of the deep-water current systems, and that there is hope that a corresponding advance will soon take place in the more difficult problems of coastal currents. The purposes of this paper are to discuss briefly the present status of the shallow-water circulation problem, to point out the more promising lines of attack, and especially to give fisheries biologists some hope that physical oceanographers will soon be able to answer some of their more pressing questions concerning fluctuations in the physical and chemical environment of coastal fisheries.

Certain general rules of coastal circulation have become well established. In the northern hemisphere the average flow is parallel to the shore line with the land on the right hand side. It follows that the average motion of the surface water is anticlockwise in a bay or gulf and clockwise around a bank. The reverse is of course true in the southern hemisphere. There is a tendency for the most pronounced surface current to be located near the 100 fathom curve, but it is also characteristic to find a second—somewhat shallower and fresher—band of current near the beach. Unfortunately, from the biological standpoint it is the rates of cross-current transport at different levels that are important, and these we know very little about as yet.

It is typical of coastal waters that salinity everywhere increases with depth. The only exceptions to this statement are to be found briefly in winter where convection has extended downward to the bottom, or where tidal stirring is especially vigorous. In any case, whether or not vertical stability is present, salinity increases gradually across the continental shelf and then increases more suddenly near the 100 fathom curve, where the contact between the relatively fresh coastal water and the more saline oceanic waters is usually located. It is also characteristic of coastal waters from the higher latitudes on the westward margin of an ocean that, throughout much of the year, there is a temperature minimum at mid-depths. The reason for this is that there is an inshore component to the flow of the bottom water, and an offshore

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component to that of the surface water. Along the whole stretch of coastline under consideration here the bottom water near the 100 fathom curve has the characteristics of truly oceanic water. That is to say, salinity approaches $35^{\circ}/_{\circ\circ}$, and temperature is at least several degrees higher than is to be found over the continental shelf at mid-depths at the latitude in question.

The temperature-minimum layer normally extends offshore as a tongue a few miles beyond the 100 fathom curve. This cold tongue overlies a maximum-salinity layer that appears to have an inshore component, and an origin well offshore in the slope-water area. The mixing processes at the contact between the coastal water and the oceanic water are by no means clear. As normally drawn from serial observations of temperature and salinity the isotherms and isohalines cross each other at a considerable angle near the extremity of the cold tongue, a pattern which is difficult to explain, if indeed it really exists. On none of the sections so far examined have sufficiently closely spaced salinity observations been secured for one to be certain of the changes in the T–S correlation curve as one moves from typical coastal water to typical slope water. It is evident that vertical mixing plays an important role near the outer limit of the coastal water.

Not only are the small-scale mixing processes near the 100 fathom curve complex and poorly understood, but also large-scale mixing processes are present. Bubbles or tongues of nearly undiluted coastal water are often encountered just below the surface layer in the slope-water area, even as far offshore as the outermost filament of the Gulf Stream System. Much less frequently has oceanic water been observed invading the area inside the 100 fathom curve, except very near the surface and close to the bottom. While the coastal water near the 100 fathom curve is clearly on the average moving towards the south and west, just beyond it the apparently detached masses of coastal water often seem to have an easterly component. In short, it is as yet impossible to describe a sector near the edge of the continental shelf in three dimensions in a reliable manner. No network of observations has been sufficiently closely spaced to permit only one solution to the contouring of the physical properties. The situation, although on a much smaller scale, may be even more ambiguous than FUGLISTER (1955) has recently shown to be the case further offshore in the Gulf Stream System.

The least complex stretch of coastal water in the area under consideration, and the one having the most sluggish circulation, is to be found between Nantucket Shoals and Cape Hatteras. Along this 500 mile stretch of coastline many rivers are continually pouring in fresh water which reaches the sea with a salinity of about $30^{\circ}/_{\circ\circ}$ after having undergone the mixing processes at work in the estuaries. In the further mixing which occurs over the continental shelf the salinity is gradually increased, both in the offshore direction and, as KETCHUM has recently shown (1955), also in the downstream direction. Since the flow past Nantucket from the Gulf of Maine is weak and probably intermittent, and since little coastal water passes Cape Hatteras, if one assigns an average salinity to the water leaving the continental shelf of 33 , and a value of 35 to the slope water inflow along the bottom, then it is evident that the offshore component must approximate 16 times the volume of all the land drainage.

As previously stated, part of this exchange between coastal and offshore waters is accomplished by small-scale mixing processes, both vertical and horizontal, and part of it by much larger eddy-type movements. The first process probably proceeds at a fairly constant rate, while the second is likely to be intermittent in character and to be triggered off by the offshore currents. It is the intermittent large-scale losses of coastal water that are probably the important events from the standpoint of a fisheries biologist. If physical processes are an important factor in the widely fluctuating annual recruitment of young fish, then it seems likely that major changes in the environment must be involved. Presumably the fish, even very young ones, are able to deal with the normal, small-scale mixing mechanisms. Thus we can ask the question: from the standpoint of a fish, what constitutes a physical catastrophy? The answer may be somewhat different for each species of fish.

The two primary variables in coastal circulation are undoubtedly the river inflow and the weather. The former supplies most of the energy, and the latter is important both in maintaining the small-scale mixing processes and also in causing the mass movements of considerable bodies of water, especially in winter. How great a variation from the normal can be produced by either factor? The larger eddying motions of an intermittent character occurring near the edge of the continental shelf are a third factor capable of producing considerable variations in the coastal environment. South of New England the available evidence indicates that these are most likely to take place along the southern edge of Georges Banks and off Chesapeake Bay. In both cases the currents of the Gulf Stream System are relatively close to the 100 fathom curve. If it is true that the offshore currents can sometimes cause relatively large eddies to form, and thus remove considerable masses of coastal water, then these events are probably not unrelated to the variations in transport of the Gulf Stream System.

If the above summary of the problem is reasonably correct, a physical oceanographer, in order to be of help to his friends concerned with fluctuations in the fisheries, needs to find answers to the following questions. By how much does land drainage have to change before the normal environment of coastal water is seriously affected? How abnormal does the weather have to become before the winds produce a corresponding change? How important to the larger-scale exchange of coastal and oceanic waters are the variations of the deep, offshore currents?

The available observations of temperature and salinity cannot be expected to yield clear-cut answers to these questions. The data consist of spot observations, separated widely in time and usually also in space. Observations from some of the extreme winters, for example 1918 and 1934, are entirely lacking. While the winds and the inflow of several of the rivers are known continuously for a good many years back, the only reasonably continuous oceanographic data are some temperature records close to the beach, and these of course mainly reflect the local weather. Offshore on the bottom where the main commercial fisheries are located we have no continuous information, nor do we have records of the variations in the offshore component of the upper half of the water column.

Why have we at Woods Hole seemingly so long avoided problems in coastal circulation? In the first place, of course, the more spectacular problems of the Gulf Stream System were close at hand. In 1933 and 1934 we did survey the Gulf of Maine on 17 occasions. Not a single paper dealing with the dynamics of the system appeared. None of us interested primarily in the causes of the circulation were able to use these extensive data to add anything of significance to Dr. BIGELOW's classical studies. Tidal currents and internal waves so complicated the picture that one could draw no important additional conclusions from the relatively complete grids of new stations.

Much improved navigation is of course now available. Underway instruments such as the bathythermograph can now provide much more detailed profiles (about 75 such profiles across the continental shelf have been accumulated), but the fact remains that nobody has had the courage to make a sustained attack on the three-dimensional mixing mechanisms going on near the 100 fathom curve. Without the help of entirely new techniques it has seemed too difficult an observational problem, and it has been clear all along that the important clues were to be found in this zone.

It is a pleasure to be able to announce here that a new programme in coastal circulation is being planned at the Woods Hole Oceanographic Institution and has already been set in motion. It has been made possible by funds supplied by the U.S. Fish and Wildlife Service, and made available to the Service by the Saltonstall-Kennedy Act. The present writer is most hopeful that this three-year study will be of real assistance to fisheries biologists, because it is planned to obtain continuous data of various kinds at several key points in the system, as well as to secure some periodic ship surveys. As KETCHUM, REDFIELD and AYERS (1951) showed so clearly in their studies of inshore waters off New York, spot observations of temperature and salinity can be illuminating if they must also satisfy some continuous requirement such as the transfer of fresh water through the network of stations. Elsewhere in this volume Dr. KETCHUM has attempted to treat the whole continental shelf area from Nantucket to Cape Hatteras as a very wide estuary. This is an important step forward in our thinking, and perhaps all that is needed to refine and to clarify the picture are some long series of current measurements at various depths.

The new programme will emphasize first of all the more systematic collection of continuous records of temperature and salinity at as many fixed points in the area as possible. The submerged recovery buoy developed by Mr. DAVID H. FRANTZ at Woods Hole will also be used for temperature observations at some critical points where moored surface buoys cannot be easily maintained. Free floating buoys carrying radio transponders will be set out and then located frequently by a plane. Continuous current measurements will be obtained at a number of points, both near the bottom and near the surface. In these ways it is hoped to gain reliable information on how strong and how persistent the winds have to be, to cause a significant disturbance in the normal exchange between coastal and offshore waters.

A recent study by CHASE (1955) has indicated that, at least in the case of young haddock, exceptionally prolonged offshore winds during the early spring can be an important factor on Georges Bank. Lacking any current measurements from the waters in which the young haddock float, CHASE was forced to use the record of the relative success of the year classes as an indicator of wind-induced currents. His reasoning, while satisfactory to a physical oceanographer, leaves something to be desired from the biological standpoint. A physical oceanographer should be able to state with conviction, on the basis of physical measurements, what the large-scale water movements have been, and then leave it to the biologists to decide whether or not these have had any biological consequences.

Once the influence of the winds and of the variations in river inflow have been properly assessed, and once the cause and importance of the large-scale mixing processes at the edge of the continental shelf have been worked out, it should be possible to go back over the available data and indicate when and where the coastal environment was seriously disturbed. The biologists are by no means satisfied that environmental changes of sufficient magnitude have occurred to account for the goings and comings of fish. It is the aim of the new programme to find means of settling this matter one way or another. Even if it only serves to bring the circulation problem into closer contact with biological needs, an important step forward will have been taken.

To summarize the present situation in coastal oceanography, our basic problems can be set forth as follows:

(1) The available data are inadequate to establish how variable the coastal environment may be because of fluctuations in its principal energy source, namely land drainage.

(2) So far as the oceanic currents are concerned, it is believed that the winds, either directly or indirectly, supply most of the energy. Considerable variations in the offshore currents are known to exist, but to what degree these influence the inshore currents remains obscure.

(3) Coastal currents, on the other hand, for the most part operate without the direct help of the winds, yet strong and prolonged winds could be a cause of important variations in the environment from the biological standpoint, especially for fishes which spawn near the edge of the continental shelf.

(4) Occasional surveys of the distribution of temperature and salinity are unlikely to provide more than limited understanding of the coastal currents, for the classical theories of physical oceanography assume steady-state conditions and, because of tidal currents, this simplification is far from being justified in coastal waters.

(5) Continuous observations, even of a rather simple sort at well-selected points over the continental shelf, should provide means of evaluating the influences of variations in river inflow, of the local winds, and of the offshore currents. Fortunately, new means of obtaining such observations have been developed in recent years.

(6) Once these factors have been evaluated, the major environmental fluctuations can probably be deduced as far back as the weather record extends.

(7) The general distribution of temperature and salinity in coastal waters indicates that, except briefly in mid-winter, it operates as a three-layered system. The warm wind-stirred surface layer and the cold stable layer just below both have offshore components, but probably quite different ones. Near the bottom, and especially where gullies and drowned river valleys exist, there is an inshore component. By moving up or down in the water column an organism can be carried either inshore or offshore. By the large-scale interaction of coastal and oceanic water it can either be carried up-coast or down-coast. From the biological standpoint it is important to establish how steady or how variable these current systems may be.

REFERENCES

BIGELOW, H. B. (1927), Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, **40** (2), 511–1027.

BIGELOW, H. B. (1933), Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. 1. The cycle of temperature. *Pap. Phys. Oceanogr. Meteorol.*, **2** (4).

CHASE, JOSEPH (1955), Winds and temperatures in relation to the brood strength of Georges Bank haddock. *J. du Cons.*, (in press).

FUGLISTER, F. C. (1955), Alternative analyses of current systems. *Deep-Sea Res.*, **2**, 213–229.

KETCHUM, B. H. and KEEN, D. J. (1955), The accumulation of river water over the continental shelf between Cape Cod and Chesapeake Bay. *Pap. Mar. Biol. and Oceanogr.*, *Deep-Sea Res.*, *Suppl.*, 3.

KETCHUM, B. K., REDFIELD, A. C. and AYERS, J. C. (1951), The oceanography of the New York Bight. *Pap. Phys. Oceanogr. Meteorol.*, **12** (1), 1–46.

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Electron microscopy in oceanographic research

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THE PHYTOPLANKTON of offshore waters is composed of unicellular species encompassing a broad size range. The larger forms are caught by fine-meshed nets, while the smaller forms are obtained by sedimentation of water samples and examined by means of inverted microscopes. After subsequent transfer to regular microscopes, the minute specimens can be examined with the best optical equipment available. Even then it is obvious that in many oceanic phytoplankton species the morphological details are too fine to be adequately observed in the light microscope. The taxonomical treatment of the nannoplankton component of oceanic populations, which includes representatives of several taxonomic groups, has, therefore, been inadequate. Recently the electron microscope has been introduced in this field and has shed light on many of the problems encountered.

As a rule diatoms are dealt with without difficulty in light microscopes, but in some cases they are so small that adequate descriptions cannot be produced. An example of this is *Fragilaria nana* Steemann Nielsen. This species forms an important part of the summer vegetation in oceanic waters of the North Atlantic, including the Norwegian Sea,(STEEMANN NIELSEN, 1935; HALLDAL, 1953). Indentification of this species and similar small diatoms is now possible by means of electron microscopy (HALLDAL and MARKALI, 1955 A).

In the case of the " guinea pig " *Nitzschia closterium* f. *minutissima*, which has been used extensively for experimental work, electron microscope observations by HENDEY (1954) have revealed that it does not belong to the diatoms at all. Consequently the numerous physiological observations on this species, now referred to as *Phaeodactylum tricornutum* Bohlin, can no longer be considered relevant for diatoms.

The extensive electron-microscopical studies of the thecal structure in diatoms (for literature see HELMCKE and KRIEGER, 1953–54) will doubtless prove useful in future marine plankton research.

The systematic group which has represented the greatest obstacle in the study of oceanic phytoplankton is the chrysophyceans and especially the coccolithophorids.

Naked chrysophyceans have been cultured, and in the electron microscope interesting morphological details of importance for the systematics of the group, such as the structure of their flagella, have been observed (PARKE, 1954).

In the study of coccolithophorids, which form such an important part of the phytoplankton in warm seas, electron microscopy has proved especially useful. The calcified coccoliths of these forms represent the most characteristic morphological feature of their cell structure, and from the time of the first description of species of this group they have been used in identification and systematical grouping. The first electron microscope pictures of coccoliths (BRAARUD and NORDLI, 1952; KAMPTNER, 1952) made it evident at once that, for this group, electron microscopy would initiate a new era for the study of taxonomy, systematics and phylogeny.

During the last few years observations have been made on approximately 50 species (for literature see HALLDAL and MARKALI, 1955 B). A new terminology for the description of the coccolith morphology has been introduced, and the first outline has been drawn up for a coccolith typology based upon electron microscope observations (BRAARUD, DEFLANDRE, HALLDAL and KAMPTNER, 1954; HALLDAL and MARKALI, 1955 B). To a large extent the old coccolith types have had to be discarded. It has also been revealed that some of the old species actually include more than one taxonomical unit. It seems obvious that, in future, electron microscopy will be indispensable when describing new species of this group.

Electron microscope observations have disclosed an unforeseen variety in the microstructure of the coccoliths, and definite taxonomic groups based upon clear-cut differences in the microstructure of the coccoliths can already be distinguished. In Pl. I and II are shown examples of some coccolith types which illustrate the striking diversity in their architecture. Species which, because of their coccolith microstructure, must be assumed to be closely related, may exhibit increasing differentiation in the coarser features of their coccolith morphology. As an example Pl. II, 1–6, shows coccoliths from four species, all of which have coccoliths of the holococcolith type, ranging from *Crystallolithus hyalinus* with its very simple coccoliths to *Homozygosphaera tholifera* with its elaborate " mitras ". In this case the microstructure of the coccoliths, which can be revealed only through electron microscopy, must form the basis for a revised systematical treatment of the group. The extremely different microstructure of such coccoliths as shown in Pl. I and II may, in time, give proof of a more complex origin of the coccolithophorids than hitherto suspected.

The study of this group with the electron microscope is at its beginning. Much work is still ahead before full advantage can be taken of this new tool, but already one may point to useful applications of these results in other fields, as for instance the study of coccoliths in rocks and in oceanic sediments of different ages.

Coccoliths form a part of sediments in the oceans, and of calcareous rocks from various periods (DEFLANDRE, 1952). In most cases the coccoliths are found detached, but since observations on the planktonic forms of today have established the specific nature of the coccolith structures, their identification is now possible through electron microscopy. Considerable work has already been done on fossil forms (for literature see DEFLANDRE and FERT, 1954). In some cases their coccoliths have been found to be identical with those of species living in the oceans today, while in other cases they are different from any yet observed in living plankton.

In examining stratification in oceanic sediments the study of the small coccoliths, which hitherto have been unidentifiable, may become most useful.

The dinoflagellates, another important group of marine phytoplankton, for the most part are large enough to be studied adequately in the light microscope. However, some oceanic species are so small that essential morphological features escape observation. *Exuviaella baltica*, a species which has a wide distribution in the North Atlantic and which forms an important component of the summer populations (BRAARUD, GAARDER and GRØNTVED, 1953; HALLDAL, 1953), has been shown to have a spiny surface structure which was quite unexpected from observations in the light microscope (see Pl. II, 7). This morphological detail may be of considerable ecological importance in view of the fact that the spines increase the absorbing surface of the cell. In part, an explanation of the wide distribution of this species and its growth in

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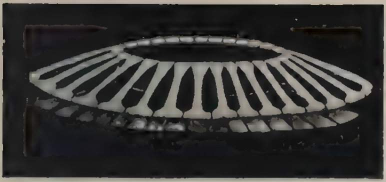

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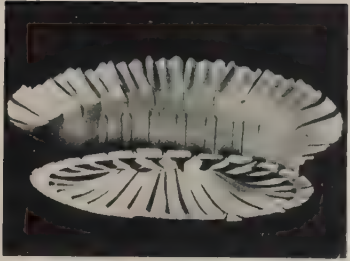

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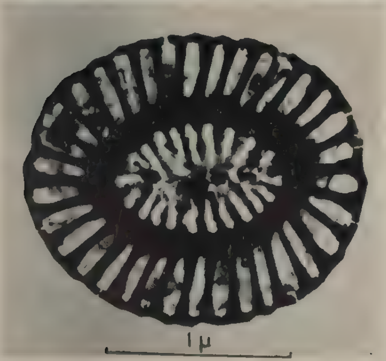

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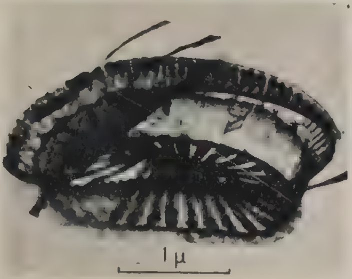

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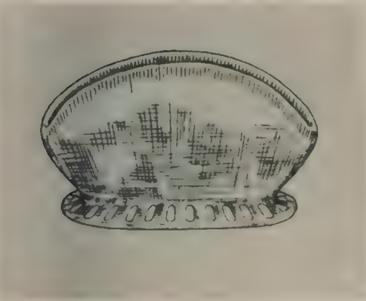

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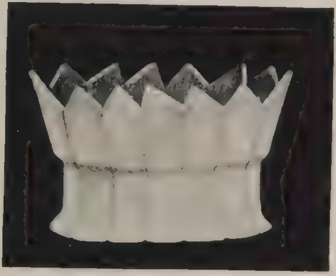

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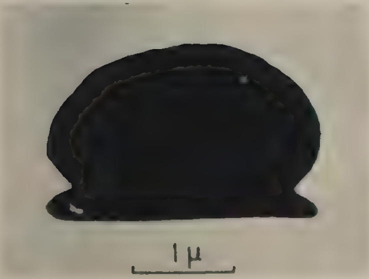

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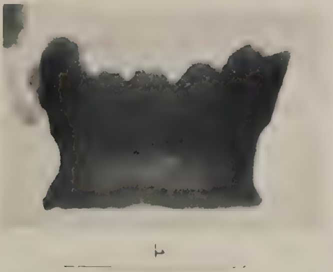

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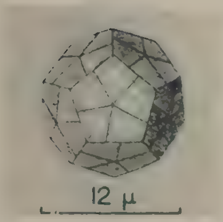
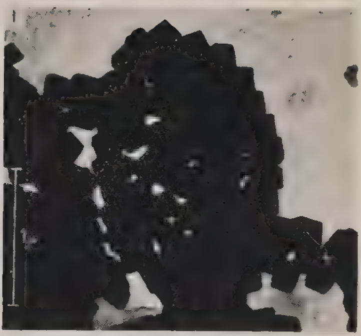
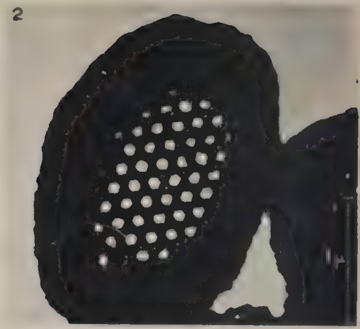
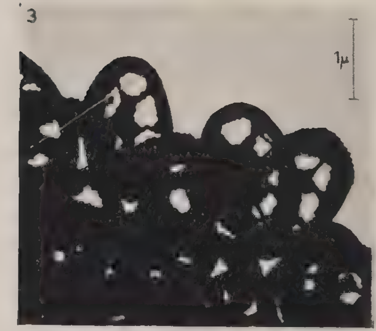
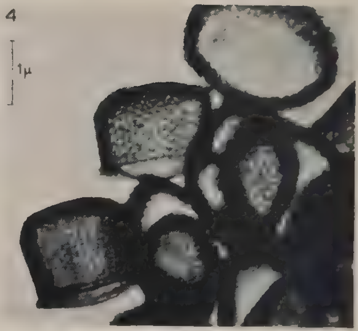


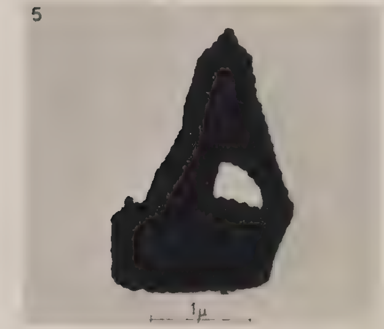
Pl. 1
1. *Coccolithus huxleyi*. (*a*) drawing and (*b*) electron-micrograph of coccolith. (From Braarud, Gaarder, Markali and Nordli, 1952.)
2. *Syracosphaera mediterranea*. (*a*) model and (*b*) electron-micrograph of coccolith. (From Halldal and Markali, 1954 b.)
3. *Anthosphaera robusta*. (*a*) model and (*b*) electron-micrograph of coccolith. (From Halldal and Markali, 1954 a.)
4. *Hymenomonas roseola*. (*a*) drawing and (*b*) electron-micrograph of coccolith. (From Braarud, 1954).
5. *Braarudosphaera bigelowi*. Drawing of cell with coccoliths (From Deflandre et Fert, 1954.)

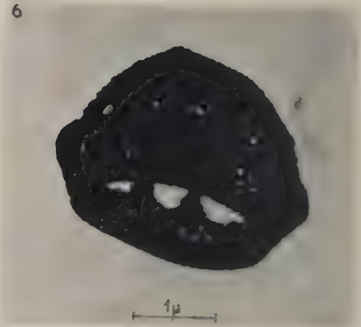


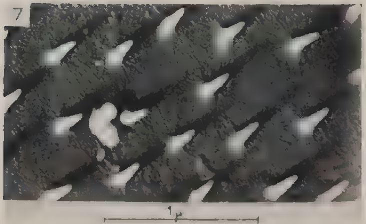












Pl. II 1. *Crystallolithus hyalinus*. Electron-micrograph of coccolith. (From GAARDER and MARKALI, 1955.)

2. *Sphaerocalyptra papillifera*. Electron-micrograph of coccolith. (From HALLDAL and MARKALI, 1954 A.)

3. *Homozygosphaera wettsteini*. Electron-micrograph of coccoliths. (By courtesy of J. MARKALI.)

4. *Calyptrosphaera oblonga*. Electron-micrograph of coccoliths. (From HALLDAL and MARKALI, 1955 B.)

5. *Homozygosphaera triarcha*. Electron-micrograph of coccolith. (From HALLDAL and MARKALI, 1955 B.)

6. *Homozygosphaera tholifera*. Electron-micrograph of coccolith. (From HALLDAL and MARKALI, 1955 B.)

7. *Exuviaella baltica*. Detail of electron-micrograph of theca. (From BRAARUD, MARKALI and NORDLI, 1955.)

waters poor in nutrients may be found in this feature (Braarud, Markali and Nordli, 1955).

Electron microscopy has opened new vistas for the student of oceanic phytoplankton populations. It will lead to a revision of the taxonomy of the many minute forms, and a sound basis for ecological surveys may thus be established. It is not difficult to foresee that in experimental studies on the physiological and ecological characters of marine phytoplankton as well, the electron microscope will turn out to be a valuable tool.

REFERENCES

Braarud, T. (1954), Coccolith morphology and taxonomic position of *Hymenomonas roseola* Stein and *Syracosphaera Carterae* Braarud and Fagerland. *Nytt Mag. Bot.*, **3**, 1–4.

Braarud, T., Deflandre, G., Halldal, P. and Kamptner, E. (1954), Terminologie, nomenclature et systématique chez les Coccolithophoridés. *Trav., VIII Congrès Int. Bot., Paris.*

Braarud, T., Gaarder, K. R. and Grøntved, J. (1953), The phytoplankton of the North Sea and adjacent waters in May 1948. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **133**, 1–87.

Braarud, T., Gaarder, K. R., Markali, J. and Nordli, E. (1952), Coccolithophorids studied in the electron microscope. Observations on *Coccolithus Huxleyi* and *Syracosphaera Carterae*. *Nytt Mag. Bot.*, **1**, 129–133.

Braarud, T., Markali, J. and Nordli, E. (1955), A note on the thecal structure of *Exuviaella baltica* Lohm. *Nytt Mag. Bot.* **4**.

Deflandre, G. (1952), Classe des Coccolithophoridés. In: *Traité de Zoologie*, ed. Pierre-P. Grassé, Masson et Cie., Paris, 439–470.

Deflandre, G. and Fert, Ch. (1954), Observations sur les Coccolithophoridés actuels et fossiles en microscopie ordinaire et électronique. *Ann. Paléont.*, **40.**

Gaarder, K. R. and Markali, J. (1955), On the coccolithophorids *Crystallolithus hyalinus* n.gen., n.sp. and *Braarudosphaera Bigelowi.* (In preparation.)

Halldal, P. (1953), Phytoplankton investigations from Weathership M in the Norwegian Sea, 1948–49, including observations during the " Armauer Hansen " cruise, July 1949. *Hvalradets Skrift., Norske Vitensk. Akad.*, **38**, 1–91.

Halldal, P. and Markali, J. (1954 a), Morphology and micro-structure of coccoliths studied in the electron microscope. Observations on *Anthosphaera robusta* (Lohm.) Kamptner and *Calyptrosphaera papillifera* Halldal. *Nytt Mag. Bot.*, **2**, 117–119.

Halldal, P. and Markali, J. (1954 b), Observations on coccoliths of *Syracosphaera mediterranea* Lohm., *S. pulchra* Lohm. and *S. molischi* Schill., in the electron microscope. *J. du Cons.*, 19 (2), 329–336.

Halldal, P. and Markali, J. (1955 a), The thecal structure of *Fragilaria nana* Steemann Nielsen. (In preparation.)

Halldal, P. and Markali, J. (1955 b), Electron microscope studies on coccolithophorids from the Norwegian Sea, the Gulf Stream, and the Mediterranean. *Avh., Norske Vitensk. Akad., Oslo*, Mat.-Naturv. Kl., (In press).

Helmcke, J. -G. und Krieger, W. (1953–54), Atlas der Diatomeenschalen im elektronmikroskopischen Bild, Berlin-Wilmersdorf, **1–2.**

Hendey, N. I. (1954), Note on the Plymouth " Nitzschia " culture. *J. Mar. Biol. Assoc., U.K.*, 33 (2), 335–339.

Kamptner, E. (1952), Das mikroskopische Studium des Skelettes der Coccolithineen (Kalkflagellaten) II. Der Feinbau der Coccolithen. *Mikroskopie*, **7**, 375–386.

Nielsen, E. Steemann (1935), The production of phytoplankton at the Faroe Isles, Iceland, East Greenland and in the waters around. *Medd. Komm. Danmarks Fisk. og Havundersogelser, Ser. Plankton*, **3** (1), 1–93.

Parke, M. (1954), New observations on marine Chrysophyceae. *Proc., VIII Congrès Int. Bot., Paris*, Sect. 17.

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 482-498.

Long-term trends and changes in the hydrography of the Faroe-Shetland Channel region

By John B. Tait

Summary—Between the years 1927 and 1952 inclusive, more or less systematic temperature and salinity observations on two roughly parallel hydrographic cross-sections of the Faroe-Shetland Channel have revealed certain fluctuations, both dynamic and characteristic, which exemplify the phenomenon of marine climatic change.

Except perhaps in 1947, the Atlantic Current through the Channel evidently flowed more strongly in the autumn-winter than in the spring-summer seasons of the period from 1946 to 1952, and these autumnal-winter intensities themselves apparently increased in magnitude to a maximum in December 1951.

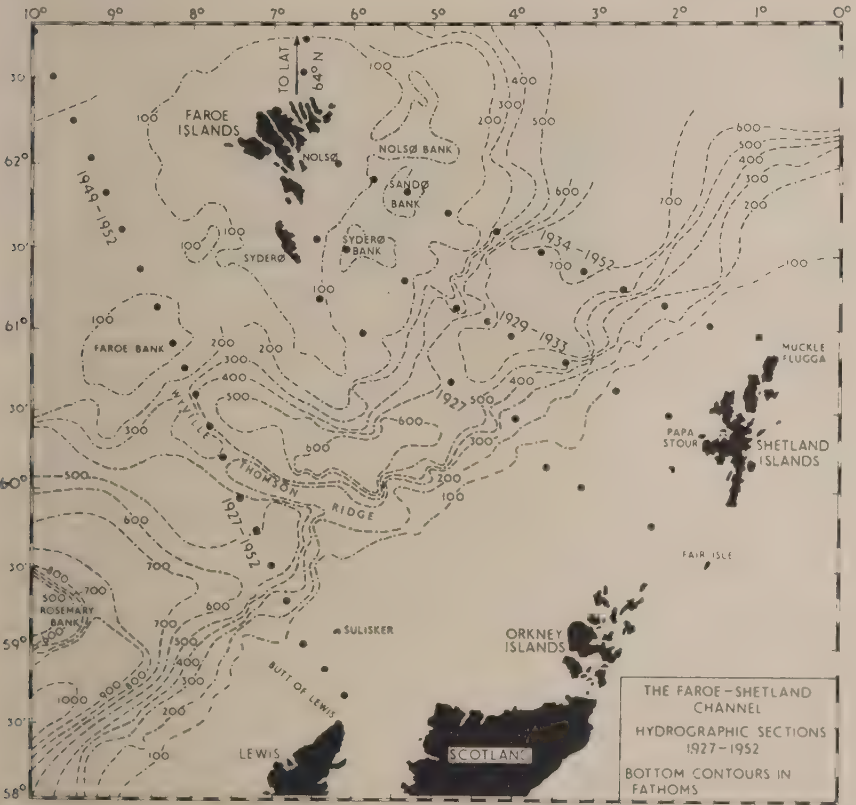
In the fourth decade, the oceanic water-mass in the Channel was infused with extra-Mediterranean water which has not appeared, save sporadically in isolated trace in the years before or since, and which from small beginnings in 1930–1931 showed maximum concentration in 1933–1934 and thereafter waned to extinction in 1938–1939.

Similar circumstances marked the appearance of first one, and then two, types of Arctic water-mass in the bottom layers of the Channel in the latter years of the fifth and the first years of the sixth decades.

Probably most oceanographers at least entertain the idea, and indeed, from much practice in a given oceanic region, many may have formed some sort of empirical conception in regard to the circulation of the oceans, to the effect that this phenomenon, besides varying seasonally and in greater or less degree annually, is subject also to longer-term fluctuation which may or may not be periodic in character. Such a conception, even discounting the probability of connection or connections between the respective phenomena, is similar to that of climatic change in regard to which much and various evidence has been adduced in recent years, e.g. glacier recession, timber line advance, seasonal mean atmospheric temperature changes, etc.

A major handicap to the adducement of oceanographic evidence of long-term fluctuation in hydrospheric conditions lies in the general inadequacy to date of the raw material of oceanographic observations. The collection and compilation of data of the necessary reliability is not yet of long duration—a prerequisite of effective research into the question of long-term fluctuation—and, moreover, has already been seriously interrupted by two world wars in those regions where it was being most intensively prosecuted. Nevertheless, it has been possible, for instance, to deduce from the trend of mean sea surface temperature in high northern latitudes that, during the past half-century or so, the Arctic region has on the whole been slowly warming up. A similar tendency to the extent of at least 0·5° C up to 1951 has recently been noted also in respect of the North Sea and English Channel regions.

Still another example of longer-term change in sea conditions than the familiar seasonal and annual variations is that instanced by Kemp (1938) in regard to the annual maximum phosphate content of English Channel waters between the third and fourth decades of the present century, with apparently correlated changes in the plankton, young fish, and, ultimately, adult fish populations of the region. These later indications, from an economic standpoint alone, point a moral which is not to be ignored, especially as much other real and circumstantial evidence points more or less strongly in the same direction. In the aggregate, this evidence which, piecemeal, tends to present a somewhat irregular and confusing picture from one region to another, and between one organic species and another, appears to fall more rationally into focus when considered from the standpoint of the characteristically different water-masses in the ocean, their fluctuations in circulation and in quantity (TAIT, 1952, p. 92).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FAROE ISLANDS
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FAROE BANK
THOMSON RIDGE
ROSEMARY BANK
SULISKER
BUTT OF LEWIS
LEWIS
SCOTLAND
ORKNEY ISLANDS
FAIR ISLE
PAPA STOUR
SHETLAND ISLANDS
MUCKLE FLUGGA
1949–1952
1934–1952
1929–1933
1927
1927–1952
100
200
300
400
500
600
700
800
900
1000
THE FAROE–SHETLAND CHANNEL
HYDROGRAPHIC SECTIONS 1927–1952
BOTTOM CONTOURS IN FATHOMS

Fig. 1

In the seas about west and north-west Europe, for example, there are permanently present at least six different and, for the most part, converging and, to some extent, intermingling water-masses. These are the oceanic, continental, Arctic, Norwegian Sea, North Sea and Mediterranean water-masses, each with its characteristic temperature, but more especially salinity, and doubtless also other properties. A variety of biological and other evidence has given rise to the conception that the most significantly important of these, at least in many respects, is the oceanic water-mass. Special attention has accordingly been directed to the oceanic incursion into European seas in an endeavour quantitatively to assess its magnitude and variations. This has been done by the normal hydrodynamic method, stemming through HELLAND-HANSEN

(1905), Hesselberg and Sverdrup (1915), Sverdrup (1933), Jakelln (1936), Jacobsen (1943), and others, from the Bjerknes' Circulation Theorem, of volume transport computation through two roughly parallel hydrographic sections laid approximately at right angles to the course of the Atlantic Current through the Faroe-Shetland Channel, scene of the pioneering oceanographical investigations of C. Wyville Thomson in 1868 and 1869, which led up to the classic *Challenger* Expedition.

There are special physical features of the Faroe-Shetland Channel region, as illustrated in Fig. 1, and of its waters, which make this a peculiarly appropriate site for an investigation of the kind indicated. As Mohn, the Norwegian meteorologist, first pointed out in 1887, by far the greater bulk, if not almost the entire mass of the oceanic water which pervades north-west European seas, flows within relatively restricted lateral limits through this Channel. It possesses, moreover, in the Wyville Thomson Ridge, a well-defined threshold from the North-Eastern Atlantic Ocean, thus defining, at its mean summit depth of about 550 metres beneath the sea surface, the thickness of the oceanic water-mass which, so far as is known, continuously passes in an east to north-easterly direction over it. Initially, then, as a first approximation, the level of zero horizontal current—the basis of conversion of relative into absolute computational values—was assumed to lie at this depth of 550 metres over the major part of a hydrographic section between the Butt of Lewis, (the northmost point of the Outer Hebrides off the west Scottish coast), and Faroe Bank, the section thus passing obliquely across the Wyville Thomson Ridge and, as nearly as may be judged, at right angles to the general course of the Atlantic Current over it. Between those stations of the section which lie over the continental shelf and slope, zero horizontal potential was assumed at the mean bottom depth between successive pairs of stations, and the modification of the computational method introduced by Helland-Hansen (1934) to suit such circumstances, applied.

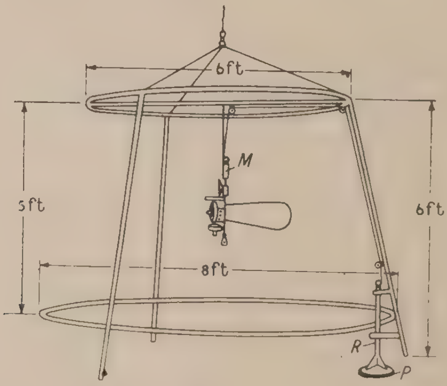

Fig. 2

As regards the assumption of zero horizontal current along the summit of the Wyville Thomson Ridge, this was experimentally confirmed in May 1953. In remarkably calm conditions, and after repeated testing in each instance at higher levels where considerable current of an order to be expected was in fact registered, an old-style but technically efficient Ekman current meter was, by means of the large, tubular, metal tripod illustrated in Fig. 2, deposited within one metre of the sea bottom, independently of the ship from which it was lowered, at no fewer than three well-spaced positions along the summit of the Ridge. The meter was activated and re-locked at precise instants by the operation of a moveable foot-plate, P, which, through its connecting rod, R, and an attached cord, released and withdrew the operative messenger M immediately on contact with, and on withdrawal from, the sea-bed. In all three instances zero current was registered during an interval of thirty minutes.

In view of the uncertainties of the normal dynamic computational method, however, the need was recognised from the outset of some form of corroboration of results obtained by its means. This was sought in similar dynamic computations of the volume transport of oceanic water through an approximately parallel and, within a matter of not more than two weeks, contemporary, hydrographic section across the debouchment of the Faroe-Shetland Channel proper into the Norwegian Sea, that is, between the Faroe and the Shetland Islands. As illustrated in Fig. 1, this section to begin with was situated in a more southerly position than that in which, from 1934 onwards, it became established.

For computation of the *absolute* oceanic volume transport through this more northerly section, in the absence of such a convenient feature as a submarine ridge as in the case of the southern section, the initial difficulty of determining the level of zero horizontal current was overcome in the light of the following reasoning.

Throughout the length of the Faroe-Shetland Channel to the Wyville Thomson Ridge, the situation has long been known, of an upper relatively warm and salt water-mass, the oceanic water-mass, over-riding a substantially colder and fresher water-mass which emanates from the deep waters of the Norwegian Sea; and also the fact that these two different water-masses move in contrary directions along the Channel. The more so, therefore, as cross-sectional representations of temperature and salinity distributions almost invariably reveal a well-marked boundary between these two water-masses, it is legitimate and reasonable to assume the existence of an interface of zero or negligible horizontal motion between them. The same diagrams in considerable number, by the obvious and increasing concentration of both isotherms and isohalines towards the isohaline of 35·00‰, which of course was zero. PETTERSSON's definition of the lower limit of demarcation of oceanic water, indicate that this isohaline probably represents in cross-section also the said interface in the Faroe-Shetland Channel of negligible or zero horizontal current. In point of fact, after trials with the isohalines of 35·05‰ and 34·95‰ as zero reference bases, and subject to one other consideration which is applicable to both sections but not altogether relevant to the present issue, but which will be mentioned in another connection below, the closest agreements between the resultant oceanic volume transports through the two sections above cited when traversed within short intervals of each other, were obtained on the basis of zero horizontal potential along the 35·00‰ isohaline on the northern section.

The fact of these agreements, most of which are very close as will be seen from Table 1, in no fewer than twenty-one instances between the years 1927 and 1952, that is, in all cases save one in which during this period the two sections were accomplished more or less together, reflects favourably on the accuracy of the above assumption. Its experimental verification by current meter with the means then at disposal—it may the more readily be accomplished now since the ingenious inventions of

CARRUTHERS (1954) for warp- or cable-angle measurement and current meter anchoring have become known,—was of course less reliable on account of the necessity to suspend the current meter from a drifting ship. Nevertheless, in the

Table I

Volume transport of oceanic water (salinity >34·99°/₀₀) through the linear hydrographic sections, (a) Faroe Bank to Butt of Lewis, and (b) Faroe Islands to Shetland (in 1927 to Fair Isle), when the pair of sections was traversed within an interval of 14 days

Year	*Inclusive dates of Sections Day/Month*		*Volume transport km³/hr*	
	(*a*)	(*b*)	(*a*)	(*b*)
1927	18/8–20/8	7/8–9/8	1·4	1·7
1929	28/5–29/5	17/5–18/5	14·0	13·2
1931	27/5–28/5	16/5–18/5	2·5	2·2
1933	20/6–22/6	9/6–11/6	3·6	2·9
1935	27/5, 5/6–6/6	15/6, 17/6–19/6	5·5	5·7
1936	28/5, 2/6–4/6	5/6, 13/6–15/6	3·9	3·9
1937	28/5–30/5, 3/6	21/5–23/5	8·8	8·8
1938	26/6–27/6, 2/7–3/7	5/7–6/7	12·8	9·6
1939	26/6–27/6	17/6–18/6	8·3	8·3
1947	18/6–19/6	10/6–12/6	19·9	19·3
1948	3/5–4/5	8/5–10/5	5·9	6·2
1949	3/9–4/9	12/9–13/9	12·4	10·0
	11/11–12/11	22/11–24/11	13·9	14·3
1950	12/5–13/5	21/5–23/5	2·5	3·4
	16/6–17/6	27/6–29/6	6·1	5·5
	19/7–21/7	2/8–4/8	4·9	3·8
1951	18/5–20/5	1/6–2/6	3·5	13·2
	16/6–17/6	7/6–9/6, 16/6	14·7	13·5
	13/7–15/7	23/7–25/7	2·6	2·0
1952	8/5–11/5	18/5–19/5	3·4	3·1
	5/7–6/7	17/7–18/7	6·8	9·8
	4/11, 8/11–9/11	17/11–18/11	11·2	10·3

remarkably calm conditions prevailing, the endeavour was made with not unsatisfactory results within a few days of the corresponding experiments on top of the Wyville Thomson Ridge in the month of May 1953. The depth of the 35·00 isohaline having been estimated as at 260 metres by rapid hydrometric measurements at a position over the lower continental slope north-west of Shetland, the result of repeated short-interval current meter suspensions to this depth yielded the inconsiderable vector of only 0·63 centimetres per second. When the more accurate salinity determinations were made it transpired that the above-estimated depth of the 35°/₀₀ isohaline at the position concerned was less by some 12 or 13 metres than the probable true depth, so that sufficiently near confirmation of the basic assumption underlying the volume transport computations on this northern section may be said also to have been achieved. Unfortunately, the favourable conditions which had prevailed to this point broke down thereafter, thus precluding further similar experimentation at other positions on the section.

Table I gives the results of the volume transport computations on the foregoing lines through the above-mentioned two Faroe-Shetland Channel cross-sections in contemporary pairs. The unit of cubic kilometres per hour has been chosen in preference to the hitherto more usual unit of millions of cubic metres per second, as affording to fishery research biologists, in whose interest these investigations were primarily carried out, a more readily grasped conception of the phenomenon of the intensity of the oceanic incursion into north-west European fishery regions.

As already indicated, the agreement between the pairs of values is remarkably close in all cases except one, namely, that for the latter half of May 1951. The immediately succeeding values, referring to the second and third weeks of June, being not only in close mutual agreement, but in agreement also with the higher of the two values for the preceding period, suggest that the disagreement in respect of this earlier period was in fact real, and significant of a radical change in the intensity of the Atlantic Current within the short interval of the two latter weeks of May 1951.

For present purposes, however, the interest of Table I is mainly in such evidence as it yields of longer than annual variations in the intensity of the Atlantic Current in the Faroe-Shetland Channel. Because of the highly disproportionate seasonal, and to a somewhat less extent annual distributions of the values, this evidence can only be regarded on the whole as of a very tentative nature.

The majority of the entries in Table I relate to the months of May, June and July, especially the two former months. Considering these values apart, their range is very considerable, namely, taking the means of paired values, from about 2·3 km^3/hr in July 1951, and 2·4 km^3/hr in May 1931, to 19·6 km^3/hr in June 1947, which in fact all but embraces the entire range of the values of Table I. It may of course be entirely fortuitous, the frequency of the values being insufficient for anything approaching positive assertion, but it can at least be observed that the highest spring-summer oceanic transports, as chronologically entered in Table I, occur in the years 1929, 1938, 1947, and 1951, that is, apparently after intervals of nine, nine, and four years respectively.

On the other hand, the lowest spring-summer values do not admit any similar inference of long-term periodicity. Their main feature in Table I would seem to be an unbroken succession of them in the six years from 1931 to 1936.

More or less in parenthesis at this still early stage in scientific oceanographical investigation, but nevertheless perhaps associated in some at present indefinable way with the subsequent phenomenon, brief notice may be taken in passing of the lowest transport value of all in Table I, namely that of 1·4 km³/hr for the third week of August 1927, and of the quite unique occurrence, so far as is known, of an iceberg within the limits of the North Sea, sighted on 23rd October 1927 about 30 miles ESE of the Outer Skerries of east Shetland (MARINE OBSERVER, 1928).

Oppositely, it may here also be pointed out that the highest transport value in Table I of almost 20 km³/hr occurred during a summer which was outstanding meteorologically over the greater part of the continent of Europe.

Further as regards the higher transports, however, it is to be noted that not all of these are recorded against the spring-summer months of May, June, and July, as witness, for instance, the figures for September and November 1949, and also that for November 1952. This feature of the results is considerably enhanced and extended when further available material is added to that of Table I. Besides the paired hydrographic sections there represented, no fewer than twenty-four single sections, a number of them traversed by the Danish research vessel *Dana*, and one due to the Norwegian vessel *Armauer Hansen*, embracing the same period of years, are available for dynamic computation on the same lines as those adopted for the Scottish sections. Single section computational results must, of course, lacking similar corroboration to those of the paired sections, be regarded as probably somewhat less reliable on that account. None the less, they are of no small value in extension of Table I, and have accordingly been incorporated along with the means of the paired values, in Table II, single section values being distinguished by an asterisk.

In this table, the high figure of 13·3 km³/hr for the month of June 1929 as derived by HELLAND-HANSEN (1934) clearly supports the mean value of 13·6 km³/hr in respect of the previous month; and the introduction of an additional year, namely 1934, on the basis of single sections only, but in no fewer than three separate assessments, in no way impairs the inference already tentatively made as regards the apparent succession of low summer oceanic transports between 1931 and 1936 inclusive. Likewise, the slightly high figure of 9·3 km³/hr for May 1938 probably anticipates in truth the subsequent increase to 11·2 km³/hr some six weeks later, and the assessments for June and July 1939 would appear to be very similarly related.

It is only from the year 1949 onwards that autumn-winter transports are available, and these, to 1952 inclusive, reveal conditions which, although hitherto perhaps occasionally suspected on empirical circumstantial evidence, are here for the first time given quantitative expression. In each of the four years concerned, the oceanic volume transports through the Faroe-Shetland Channel were evidently of greater intensity than the preceding spring-summer incursions. It is material also that the years are consecutive, for, from the standpoint of long-term variations, it would almost appear from the values given that the successive autumnal accessions to the intensity of the oceanic influence in the Channel themselves increased annually to a high maximum in December 1951. It can be taken as practically certain that the phenomenon of greater autumn-winter than spring-summer oceanic transports is not an annual occurrence, the combination of circumstantial with the factual evidence of Table II and such assessments as are available for earlier years (HELLAND-HANSEN, 1905, and ROBERTSON, 1905, 1907, 1909a, 1909b, 1913), suggesting that this oceanographic feature, like that of the succession of low summer transports between 1931 and 1936 inclusive, occurs in groups of years, and recurs only at more or less long-term intervals of the order each of at least several years. Qualitative evidence in

Table II

Oceanic volume transport through the Faroe-Shetland Channel

Year	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
1927						Km^3/hr.		1·5				
1929					13·6	13·3*						
1931					2·4							
1933						3·3						
1934				4·8*	4·4*		3·1*					
1935						5·6						
1936						3·9						
1937					8·8							
1938					9·3*	11·2						
1939						8·3	10·4*					
1946								5·0*				
1947						19·6	15·8*					
1948					6·1	8·9*		4·7*				
1949			7·3*	5·2*			11·5*		11·2		14·1	
1950			15·7*		3·0 4·2*	5·8	4·4	3·7*			12·3*	
1951					3·5*	13·8	2·3	2·7*	10·0*	10·8*		23·4*
1952		11·9*	14·5*		3·3	7·5	8·3				10·8	

* Single section results

support of the suggestion is contained in another aspect of the results of this comprehensive investigation of the hydrography of the Faroe-Shetland Channel which is about to appear elsewhere* *in extenso*.

It was mentioned earlier that the remarkably close agreements recorded between the contemporary paired sections across the Channel depended also in a number of cases, and as it turned out depended very materially in some instances, on a certain condition which referred to both sections. This condition was the re-inclusion of apparently aberrant original observations of temperature or salinity, principally the latter, which by former standards were customarily excluded, or replaced by interpolation from smooth curves, if they implied more or less radical inversion of density in the vertical water column. In the present investigation, the years in which this condition of reinsertion of such observations had most frequently to be applied were those between 1931 and 1936 inclusive, when considerable numbers of high and even of extraordinarily high salinity values were registered, of maximum magnitude and frequency in the year 1933 in the Faroe-Shetland Channel, in 1934 in the northern North Sea, and almost without exception as subsurface values. It was in the latter region, in fact, that these recurring abnormally high salinity records were first

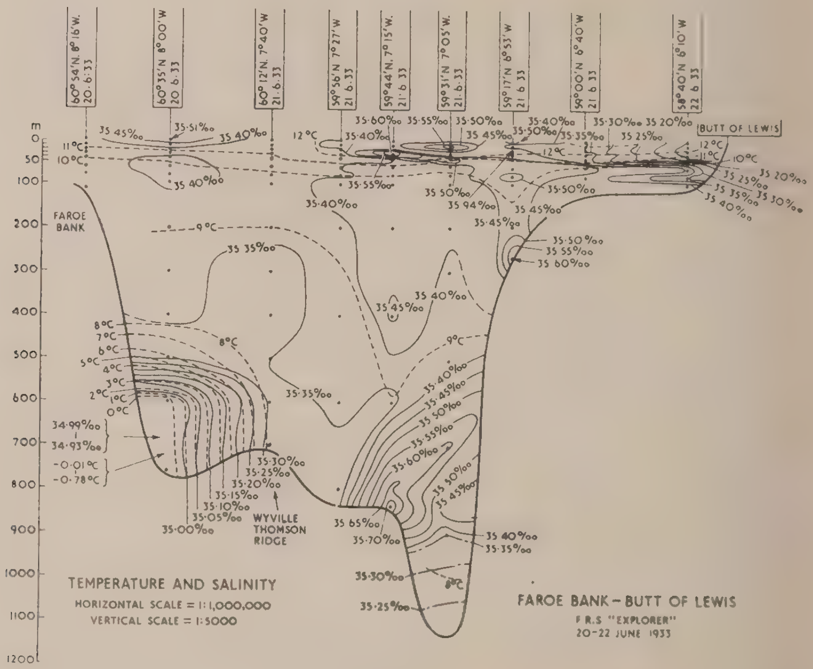

Fig. 3

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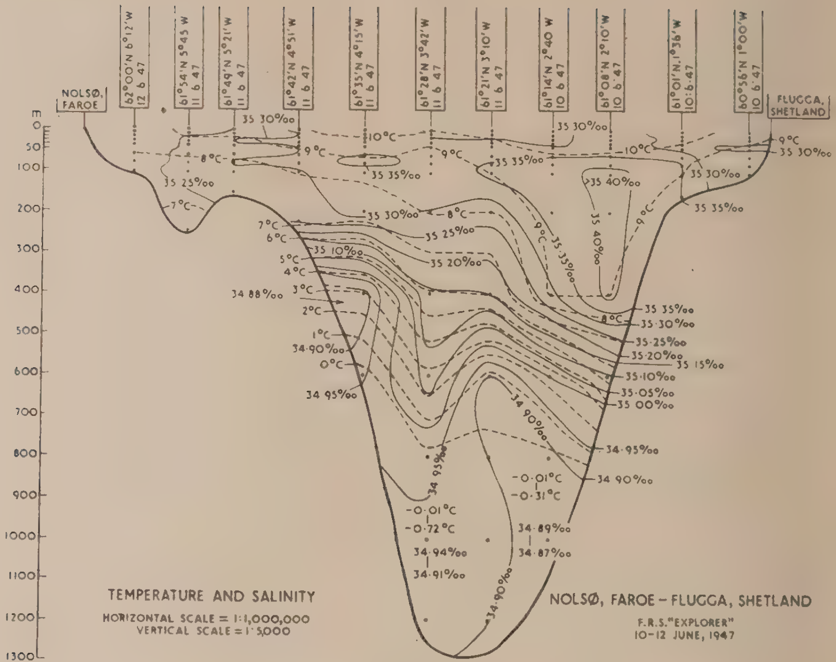
* In the Scottish Home Department's series of " Marine Research " publications.

noticed and recognised, after investigation (Tait 1935), to be true records, indicative, it was then empirically concluded, of abnormally powerful oceanic incursion into the region. As illustrated in Figure 1 of this reference, a not insignificant aspect of the geographical incidence of these abnormal northern North Sea salinity observations in adducement of evidence towards their reality, links that particular research with the results of an investigation into the current system of the region (Tait, 1937).

The dynamic results of Table II, however, in respect of the Faroe-Shetland Channel, belie the earlier conclusion reached in interpreting these abnormal North Sea observations, clue to the origin and meaning of which was found on the Butt of Lewis to Faroe Bank hydrographic section of June 1933 (Fig. 3). Here, on and off the southern slope of the Wyville Thomson Ridge, there occurred in the depths of 840 metres and 700 metres at two adjacent stations the high salinities of 35·73‰ and 35·61‰ respectively, with related high observations, although of lower order, both above and below the latter especially. The two outstanding values, in conjunction with the simultaneously recorded temperatures at the same depths, furnish densities (σ_t) of 27·74 and 27·63 respectively, that is, within the bracket which Sverdrup, Johnson, and Fleming (1942, p. 670) cite as characteristic and significant of the North Atlantic Ocean intermediate layer of so-called Mediterranean water effluent. It is clear from Fig. 3 that the above salinity records signify the core of such a body of Mediterranean water impinging upon the southern slope of the Wyville Thomson Ridge, and thereby, by the consequent turbulent motion which the trends of isotherms, and especially of isohalines, almost invariably indicate in this region, becoming disintegrated, to appear in the upper water levels northward of the Ridge,—but only extremely seldom at the surface—as isolated high salinity nuclei within the body of the oceanic water-mass, the maximum salinity of which here normally lies between 35·35‰ and 35·45‰. Such isolated nuclei did in fact occur on the Faroe-Shetland Channel sections of 1931 (as Table II indicates, there was no 1932 section), 1933, 1935, 1936, and 1938, being absent, however, from the 1934 and 1937 sections. Despite the increased frequency of traverse of these sections since 1946, high salinity values suggestive of Mediterranean water intrusion into the oceanic water-mass have occurred only sporadically, as in May 1948, August 1951, and November 1952, and then only as singular records on the southern section over the threshold to the Channel. It may be that, by application of the principle of discarding apparently aberrant observations, previous indications of the presence of Mediterranean water in the Faroe-Shetland Channel, and even within the northern North Sea, have thus been lost. It is safe to say, however, that this is a phenomenon which, substantially, occurs only once in a while, and probably, as in the fourth decade, in groups of years, in other words it is a phenomenon of only long-term recurrence.

Yet another example, this time with reference to the deep waters of the Faroe-Shetland Channel, may be cited from this investigation as suggestive of probably similar long-term fluctuation. What have hitherto been accepted as the normal deep water temperature and salinity distributions in the Channel, i.e., below the oceanic water-mass, are almost uniform conditions in both characters, namely, thermal registrations at or near zero temperature Celsius, and salinity records of around 34·92 to 34·94. These properties define the origin of the deep Channel water as from deep levels of the Norwegian sea to the northward. Since the effective commencement of observations in the Faroe-Shetland Channel at the beginning of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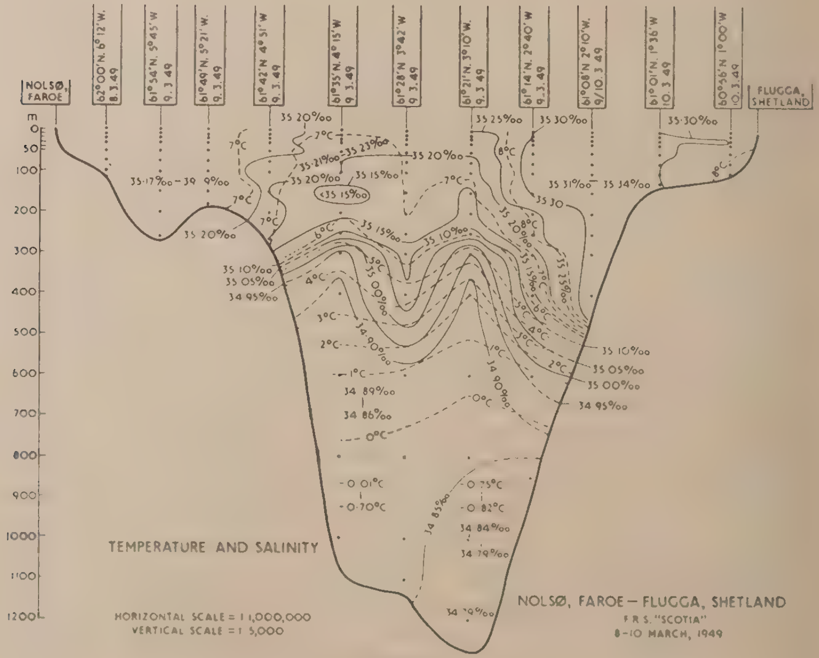
TEMPERATURE AND SALINITY
HORIZONTAL SCALE = 1:1,000,000
VERTICAL SCALE = 1:5,000
NOLSØ, FAROE – FLUGGA, SHETLAND
F.R.S. "EXPLORER"
10–12 JUNE, 1947

Fig. 4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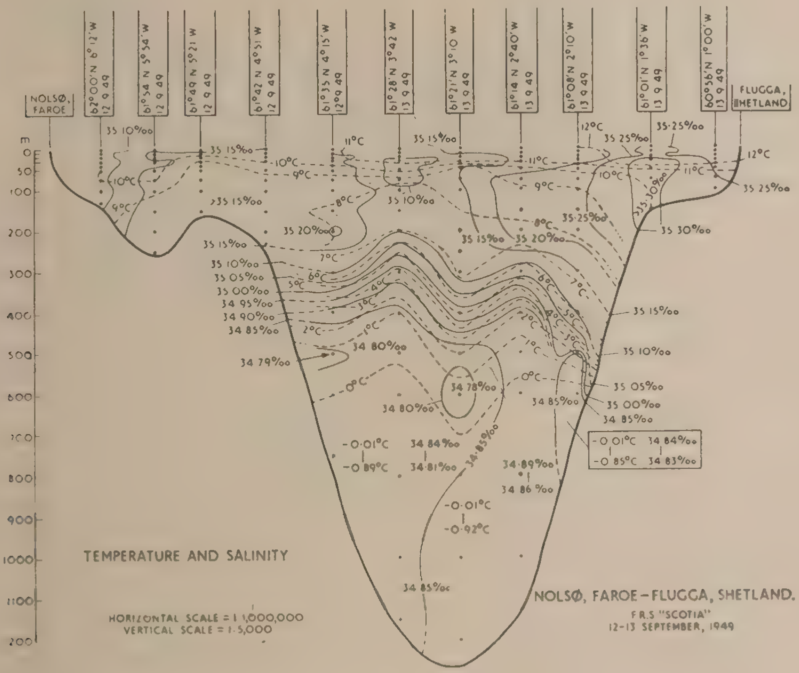
TEMPERATURE AND SALINITY
HORIZONTAL SCALE = 1 1,000,000
VERTICAL SCALE = 1 5,000
NOLSØ, FAROE – FLUGGA, SHETLAND
F.R.S. "SCOTIA"
8–10 MARCH, 1949

Fig. 5

the present century, little if any specific notice has been taken of the relatively infrequent occurrence of salinity values below 34·90$^{\circ}/_{oo}$. There is, however, clear evidence in the tabulated observations of a frequency concentration of such low salinity records. from 34·82$^{\circ}/_{oo}$ to 34·88$^{\circ}/_{oo}$ with occasional instances of 34·76$^{\circ}/_{oo}$ to 34·79$^{\circ}/_{oo}$, in the years between 1907 and 1910 inclusive, such as occurred again towards the end of the fifth and the beginning of the sixth decades.



TEMPERATURE AND SALINITY

HORIZONTAL SCALE = 1 1,000,000
VERTICAL SCALE = 1·5,000

NOLSØ, FAROE – FLUGGA, SHETLAND.
F.R.S "SCOTIA"
12-13 SEPTEMBER, 1949

Fig. 6

Apart from a singular, isolated, 34·87$^{\circ}/_{oo}$ salinity record in July 1934, no Faroe-Shetland deep water salinity value below 34·90$^{\circ}/_{oo}$ was encountered in the years between 1931 and 1939 inclusive. Similar isolated results were again evident in July and August 1946, but by the month of June 1947 (Fig. 4) almost one-half of the deep water mass underlying the oceanic water-mass was of the relatively low salinity of 34·87$^{\circ}/_{oo}$ to 34·89$^{\circ}/_{oo}$, and had a higher minimum temperature than the neighbouring deep Norwegian Sea water-mass. It seems clear from HELLAND-HANSEN and NANSEN (1909) that this low salinity (34·86$^{\circ}/_{oo}$–34·89$^{\circ}/_{oo}$) intrusion into, and sometimes displacement of, the deep Norwegian Sea water-mass of the Faroe-Shetland Channel, is Arctic water emanating from the deeper layers of the East Icelandic Arctic Current and found in depths of about 300 to 400 metres " from the continental slope off the east coast of Iceland along the slope of the Faroe-Iceland Ridge and off the Faroes, past the Faroe-Shetland Channel." Evidently, however, this Arctic water layer does

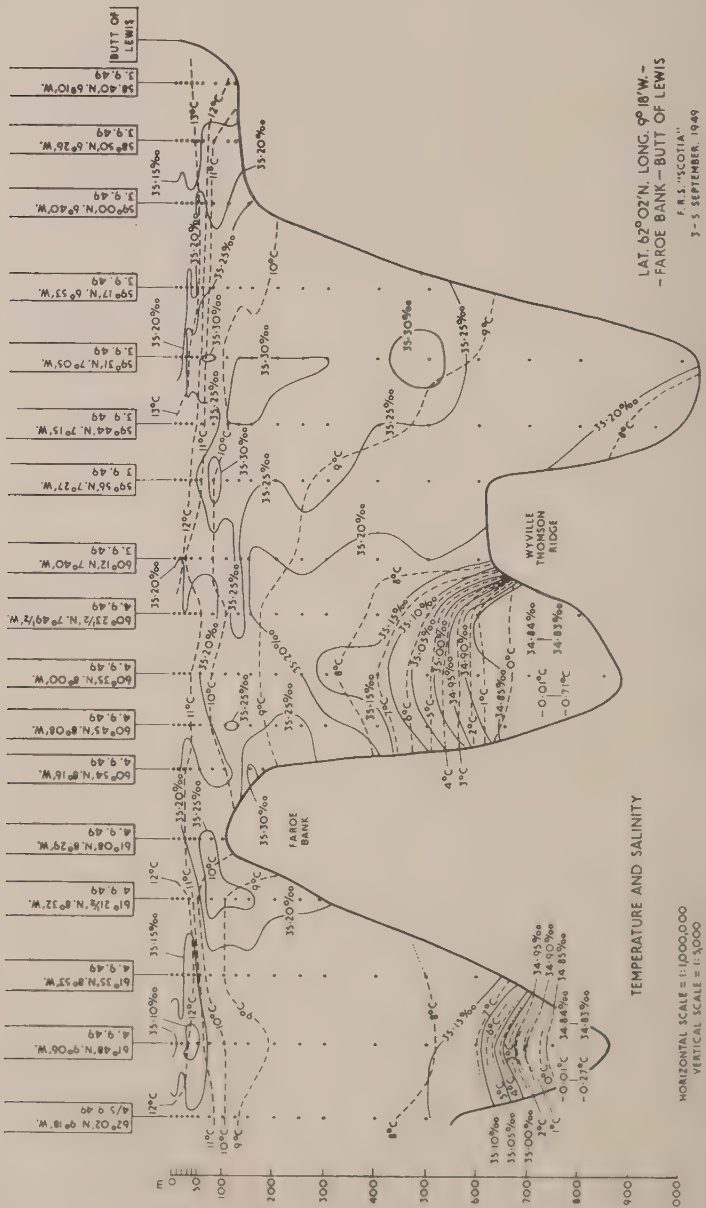


Fig. 7

not in fact at all times bypass the Channel in its eastward trend across the southern reaches of the Norwegian Sea.

Except for a single 34·89‰ record in August 1948, this year appears to have been devoid of any Arctic water in the Channel, but in early March 1949 (Fig. 5), deep water conditions there were radically different from those normally anticipated. The expected Norwegian Sea water bottom layer was then entirely displaced below about 350 to 700 metres by the Arctic water-mass, being sandwiched in a narrow undulatory band in cross-section between it and the uppermost oceanic water-mass. Not only so, but apparently still another water-mass of still lower temperature and lower salinity (34·79‰ to 34·84‰) than the above-defined Arctic water-mass seems to have underlain to some extent the latter in the deepest part of the Channel against the bottom of the continental slope. There is sufficient reason to designate this new water-mass surface Arctic water, thus distinguishing it from the intermediate Arctic water-mass immediately above it in the Channel region. At the end of April 1949 the intermediate Arctic water-mass was located at the southern extremity of the Channel, in its toe, so to speak, between the Wyville Thomson Ridge and the Faroe Bank. Five months later, in September 1949 (Fig. 6), not only did surface Arctic water occupy more than half of the deep-water cross-sectional area of the northern part of the Channel, the two Arctic water-masses together there again 'supporting' only a narrow band of Norwegian Sea water beneath the oceanic mass—except against the continental slope where surface Arctic water appears to have been directly contiguous

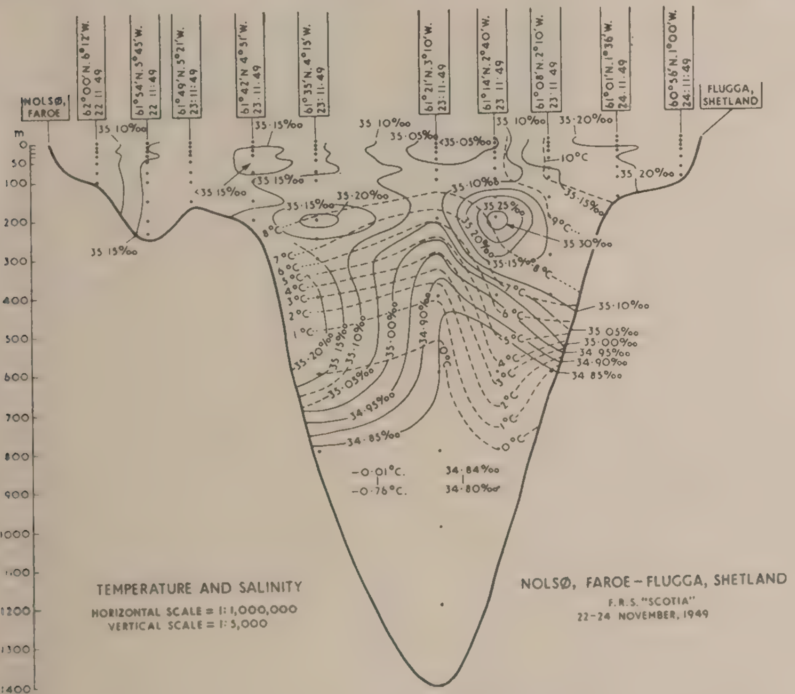
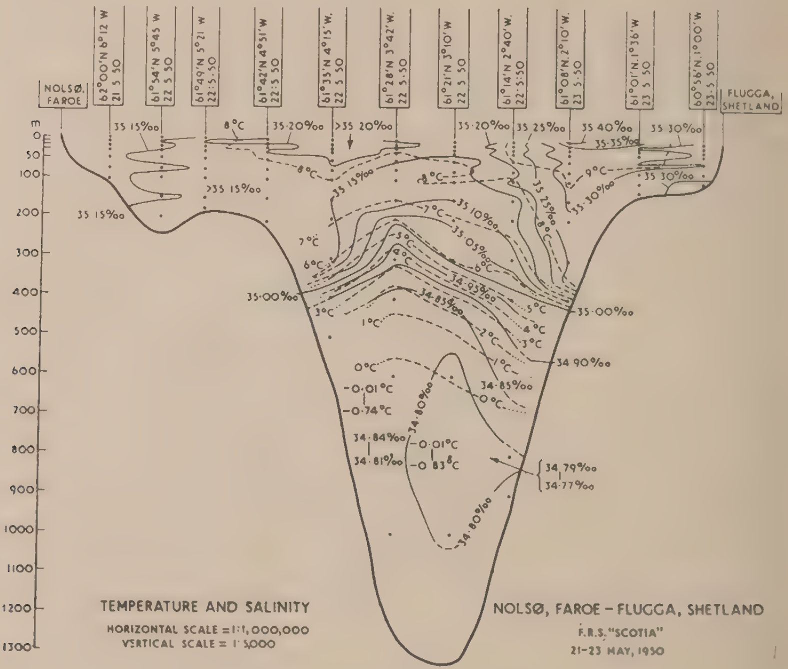


Fig. 8

with the underside of the oceanic layer—but surface Arctic water also, as distinct from intermediate Arctic water, was encountered in the deep toe of the Channel as well as in similar depths of the other, i.e. north-western, side of Faroe Bank, the Butt of Lewis to Faroe Bank section having on this occasion been extended considerably northwestwards (Fig. 7).

By November of the same year (Fig. 8), the surface Arctic water-mass *totally* underlaid intermediate Arctic, Norwegian Sea, and oceanic waters across the northern part of the Channel, there being relatively very little apparently of either of the two sandwiched water-masses present at all.



TEMPERATURE AND SALINITY
HORIZONTAL SCALE = 1:1,000,000
VERTICAL SCALE = 1:5,000

NOLSØ, FAROE – FLUGGA, SHETLAND
F.R.S. "SCOTIA"
21–23 MAY, 1950

Fig. 9

This was still relatively the position in the latter half of May 1950 (Fig. 9) with, however, a substantial cross-sectional area of still lower (34·79°/oo–34·77°/oo) salinity water within surface Arctic mass, probably indicating still more intensive influence from this source than in the previous year in the deeper Channel layers. By the beginning of the following August there were signs on the northern section of Norwegian Sea water beginning to displace both types of Arctic water along the continental slope to the considerable depth of nearly 1,100 metres, although the latter, i.e. the Arctic waters, still formed the main bulk of the bottom waters over the greater part of the section.

Three months later, in November 1950, only the intermediate Arctic water-mass and no surface Arctic water, was found on the northern section, and even this was in process of cleavage in mid-section by Norwegian Sea water as illustrated in Fig. 10.

The intermediate Arctic water-mass was entirely absent from the toe of the Channel by May 1951, and almost totally excluded by Norwegian Sea water from the depths of the northern section in June. There was no evidence whatever of its presence on the same section by the month of October, and only an isolated trace appeared two months after.

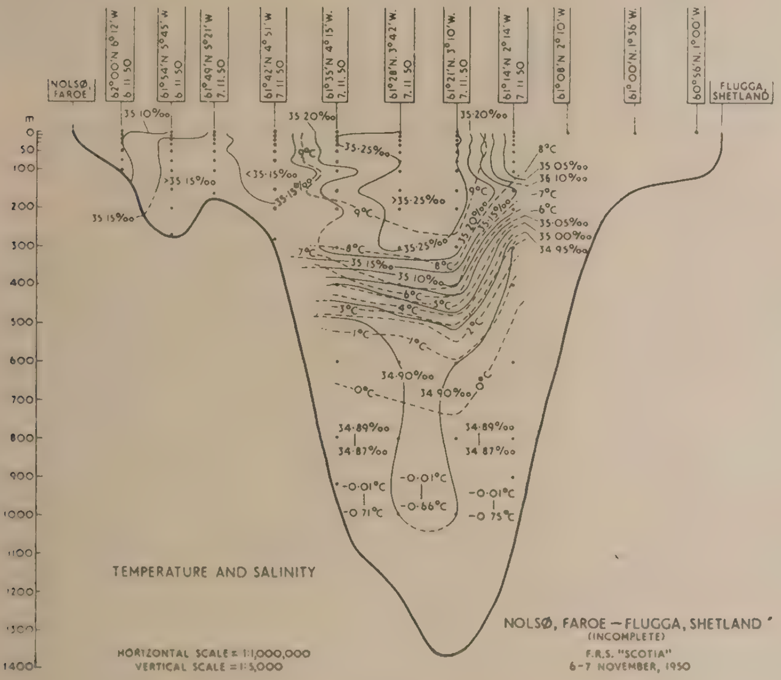


Fig. 10

A return of both Arctic water types was recorded along the entire length of the Faroe-Shetland Channel in May and June 1952, but both were obviously receding from the region one month later, and towards the end of the year had left only isolated " nuclear " traces within the Norwegian Sea water-mass.

Once again, then, a phenomenon has been witnessed over a group of years which seems not to have been in evidence for at least a number of years previously: and at all events in respect of the Faroe-Shetland Channel region, the conception of long-term trends and changes in hydrographic, including dynamic, conditions seems amply to be in accordance with observational facts. Only systematic and sufficiently intensive and continuous observations on similar lines to those practised in the past few years particularly can serve further to elucidate these interesting and doubtless, in several respects, more or less highly important geophysical phenomena.

REFERENCES

CARRUTHERS, J. N. (1954), Some inter-relationships of oceanography and fisheries. *Arch. Meteorol., Geophys. u. Bioklim.* (B), **6** (1/2), 167–189.

CARRUTHERS, J. N., WOODS, A. J. and LEE, A. J. (1954), On the instrumental measurement of line shape under water. *Deutsche Hydrogr. Zeits.*, **7** (1/2), 22–35.

HELLAND-HANSEN, B. (1905), Report on the hydrographical investigations in the Faroe-Shetland Channel and the northern part of the North Sea in the year 1902. *North Sea Fish. Invest. Comm. Northern Area*, 1902–1903, *Rept.* No. **1**, 1–50.

HELLAND-HANSEN, B. (1934), The Sogne Fjord section. In: James Johnstone Memorial Volume, Liverpool Univ. Press, 257–274.

HELLAND-HANSEN, B. and NANSEN, F. (1909), The Norwegian Sea: its physical oceanography based on the Norwegian researches. 1900–1904. *Rept. Norwegian Fish. Mar. Invest.*, **2** (1), 1–390.

HESSELBERG, TH. and SVERDRUP, H. U. (1915), Beitrag zur Berechnung der Druck-und Massenverteilung im Meere. *Bergen Museums Aarbok*, No. **14**, 1–18.

JACOBSEN, J. P. (1943), The Atlantic Current through the Faroe-Shetland Channel, and its influence on the hydrographical conditions in the northern part of the North Sea, the Norwegian Sea and the Barents Sea. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer.*, **112**, 5–47.

JAKELLN, A. (1936), The water transport of gradient currents. *Geofys. Publ., Norske Videnskaps-Akad., Oslo*, 11 (11), 1–14.

KEMP, S. (1938), Oceanography and the fluctuations in the abundance of marine animals. Presidential Address, Sect. D, *British Assoc. Adv. Sci., Rept. Ann. Meet.*, 1938, 85–101.

MARINE OBSERVER (1928), Summary of ice conditions during 1927. *Mar. Obs.*, **5** (52), 75. April, 1928. Meteorological Committee, Air Ministry, London.

MOHN, H. (1887), The North Ocean, its depths, temperature and circulation. *Norwegian North Atlantic Exped.*, 1876–1878, **2**, 1–212.

ROBERTSON, A. J. (1905), Report on hydrographical investigations in the Faroe-Shetland Channel and the northern part of the North Sea in 1903. *North Sea Fish. Invest. Comm., Northern Area, Rept.* No. **1**, 51–114.

ROBERTSON, A. J. (1907), Report on hydrographical investigations in the Faroe-Shetland Channel and the northern part of the North Sea during the years 1904–1905. *North Sea Fish. Invest. Comm., Northern Area, Rept.* No. **2**, 1–140.

ROBERTSON, A. J. (1909A), Report on the hydrographical investigations in the North Sea and Faroe-Shetland Channel during the year 1906. *North Sea Fish. Invest. Comm., Northern Area, Rept.*, No. **4**, 1–60.

ROBERTSON, A. J. (1909B), Report on hydrographical investigations in the North Sea and Faroe-Shetland Channel during the years 1907–1909. *North Sea Fish. Invest. Comm., Northern Area, Rept.* No. **4**, 143–196.

ROBERTSON, A. J. (1913), Report on hydrographic investigations in the North Sea and Faroe-Shetland Channel during the years 1909–1910. *North Sea Fish. Invest. Comm., Northern Area, Rept.* No. **5**, 337–404.

SVERDRUP, H. U. (1933), Vereinfachtes Verfahren zur Berechnung der Druck-und Massenverteilung im Meere. *Geofys. Publ., Norske Videnskaps-Akad., Oslo*, **10** (1), 1–9.

SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. H. (1942), The oceans; their physics, chemistry and general biology. New York, Prentice-Hall, Inc., 1087 pp.

TAIT, J. B. (1935), Recent high salinity records from the northern North Sea. *Rapp. Proc. Verb., Cons. Perm. Int. Expl. Mer*, **94** (III, 8), 60–65.

TAIT, J. B. (1937), The surface water drift in the northern and middle areas of the North Sea and in the Faroe-Shetland Channel. *Fish. Bd., Scotland, Sci. Invest.*, 1937 (1), 1–60.

TAIT, J. B. (1952), Hydrography in relation to fisheries. London, Edward Arnold & Co., 106 pp.

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